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MSc

Foraging areas and associated environmental preferences of juvenile loggerhead turtles (*Caretta caretta*)

Bárbara Maria Azevedo do Carmo Canhoto

Dissertação de Mestrado apresentada à
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Mestrado em Recursos Biológicos Aquáticos
Departamento de Biologia
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Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

Porto, _____/_____/_____

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Para ti, pai…

ABSTRACT

The tracks of 10 juvenile loggerhead turtles that were tagged in 1998, in Madeira (Portugal) were analysed, to determine foraging regions and associated environmental preferences. To smooth the paths and standardize the locations in time, a Kalman-based (KF) state space model (SSM) was applied to the raw data. Area-restricted search (ARS) was used as a proxy for foraging behaviour, and three methods were combined to determine ARS: first passage time (FPT), straightness index (SI) and speed (corrected with currents direction and magnitude).

Environmental key variables that may be related with foraging choices of these animals were extracted, using Marine Geospatial Ecology Tools (MGET), in ArcMap™ (ESRI 2011). Based on previous works concerning loggerheads and other marine vertebrates, the chosen variables were: bathymetry, sea surface temperature (SST), sea surface height (SSH), sea surface height anomalies (SSHA) and chlorophyll *a* (Chl*a*) concentration.

A generalised additive model (GAM) was applied to the data, to determine the relation between the response variable (ARS) and the predictors (environmental variables).

Results showed the existence of a relationship between the environmental variables and foraging regions, identified by both visual analysis of the data and by the model results. In general, the animals foraged in regions where one or more of these features occurred: low bathymetry, absolute high values of sea surface height anomalies and also within the boundaries of sea surface temperature fronts and Chl*a* fronts. Most animals also headed in opposite directions, according to the season they were tagged (spring or autumn), demonstrating latitude ranging variability by season. The combination of the methods applied to determine ARS was successful in allowing to relate the environmental variables with foraging locations and also enabled obtaining a visual scale for ARS locations. Results of this work will be used for comparison in an ongoing larger study related with sunfish (*Mola mola*) foraging habits.

Key-words: Foraging behaviour, Loggerhead turtle, *Caretta caretta*, Atlantic Ocean, ARGOS satellite telemetry, Area-restricted search, Generalised additive model

RESUMO

Os percursos de 10 juvenis da espécie Tartaruga-comum (*Caretta caretta*), marcadas em 1998, na Madeira, foram analisados, com o intuito de serem detectadas regiões onde os animais se alimentaram e determinar as variáveis ambientais associadas a esse comportamento. Para tal, os percursos foram inicialmente suavizados e as posições regularizadas no tempo, através de um Modelo de estado no espaço (SSM), baseado no filtro de Kalman (KF). A pesquisa em área restrita (ARS) foi utilizada como indicador de comportamento alimentar das tartarugas e, para determiná-la, três métodos foram combinados: tempo de primeira passagem (FPT), índice de linearidade (SI) e a velocidade dos animais ao longo dos seus percursos, corrigida com a direcção e magnitude das correntes marítimas. Utilizando a ferramenta "Marine Geospatial Ecology Tools" (MGET), as variáveis ambientais de interesse foram extraídas, no ArcMap™ (ESRI 2011). As variáveis foram seleccionadas tendo por base trabalhos existentes, respeitantes à espécie e a outros vertebrados marinhos. Assim, foram extraídas as seguintes variáveis: batimetria, temperatura da superfície do mar (SST), altura da superfície do mar (SSH), anomalias da altura da superfície do mar (SSHA) e concentração de clorofila *a* (Chl*a*). Para determinar a relação existente entre as variáveis ambientais (variáveis explanatórias) e as regiões de alimentação (representadas pelas posições de ARS – variável de resposta), um modelo aditivo generalizado (GAM), foi aplicado aos dados. Os resultados demonstram a existência de uma relação entre as variáveis ambientais e o comportamento alimentar das tartarugas, identificada tanto pela visualização dos dados no ArcMap™ (ESRI 2011), como pelos resultados do modelo. Em geral, os animais alimentaram-se em regiões onde uma ou mais das seguintes situações se verificou: baixa batimetria, valores (absolutos) elevados das anomalias da altura da superfície do mar e ainda em frentes térmicas e frentes de Chl*a*. A maior parte dos animais também se dirigiu para latitudes opostas, de acordo com a estação do ano em que foram marcados (Primavera ou Outono), demonstrando existir variabilidade, entre estações, nos limites de latitude utilizados. A combinação dos métodos utilizados para determinar a ARS permitiu relacionar o comportamento alimentar dos animais com as variáveis ambientais e ainda obter uma escala visual de posições de ARS. Os resultados deste trabalho serão utilizados para comparação num projecto de maiores dimensões, cujo tema está relacionado com aspectos alimentares do Peixe-lua (*Mola mola*).

Palavras-chave: Comportamento alimentar, Tartaruga comum, *Caretta caretta*, Oceano Atlântico, Telemetria de satélite ARGOS, Pesquisa em área restrita, Modelo aditivo generalizado

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LIST OF ABREVIATIONS

ARGOS - Advanced Research and Global Observation Satellite

ARS – Area-restricted search

Chl*a* – Chlorophyll *a*

FPT – First passage time

GAM – Generalised additive model

KF – Kalman filter

SI – Straightness Index

SST – Sea surface temperature

SSH – Sea surface height

SSHA – Sea surface height anomalies

1 – INTRODUCTION

1.1 – Foraging Behaviour and Area-restricted search (ARS):

Animals' foraging behaviour has been studied for many years, and related analyses provide a better knowledge of both feeding regions to be preserved, for conservation purposes, as well as animals' habitat preferences (e.g., environmental choices, potential preys). According to Barceló (2011), many threats to marine predators are likely to take place during foraging, which makes the identification of this activity essential for critical habitat designation, and it is of great importance for fisheries management and marine reserve planning.

Understanding animal movements and how they relate to environmental variability is a subject that has captured the attention of many researchers over the last decades (Holden 2006, Nathan et al. 2008, Schick et al. 2008, Postlethwaite et al. 2013). Identifying critical habitat through the analysis of the relationships between movements and environmental variables has become a common approach for spatial management of commercial or endangered species (Hobday et al. 2010, Block et al. 2011, Žydelis et al. 2011, Abecassis et al. 2013).

One common reason for analysing animal movement data is to discover hidden information about behaviour that cannot be directly observed (Postlethwaite et al. 2013), as it is rare and highly difficult to observe specific behaviours associated with successful foraging (Tinker et al. 2007). For that reason, indirect foraging metrics have been widely applied both in terrestrial and marine ecosystems, in which a movement path of an animal is, for example, split into its track segments and analysed for potential locations that are representative of a certain behaviour (e.g. foraging versus not foraging) (Barceló 2011).

The last two decades have seen a marked increase in research by using tracking technologies to understand the ecology and behaviour of animals (Phillips et al. 2007, Tremblay et al. 2007, Aarts et al. 2008, Schick et al. 2008, Tancell et al. 2013). Second only to time-depth records, tracking data are likely the most abundant source of at-sea animal behaviour data (Robinson et al. 2007).

Observed tracks typically consist of a time series of positional information and often the real interest focuses on characterisation of different behavioural states (e.g., resting, commuting, foraging) and how they change over time (Postlethwaite et al. 2013). In order to characterise foraging behaviour using tracking data, it is necessary to quantify and validate track parameters as feeding proxies (Robinson et al. 2007). For that purpose, a variety of

track-based methods has been widely used to extract valuable information (such as the spatial extent of migrations and the location of feeding areas, for example) from telemetry data (Robinson et al. 2007). Mapping of such areas often involves kernel analysis (Boyd et al. 2008, Wilson et al. 2009), while inferences about animal behaviour from path characteristics and the use of space can be made using first passage time analysis (Suryan et al. 2006, Pinaud 2008), fractal analysis (Laidre et al. 2004, Tremblay et al. 2007) and state-space modelling (Patterson et al. 2008, Hart et al. 2010, Jonsen et al. 2013).

Robinson et al. (2007), suggested that feeding could be inferred at least in part from the observation of localized areas of movement at sea, assuming that an animal will preferentially spend more time in regions of successful feeding. Predators searching for patchily distributed prey are expected to move in more twisted ways in areas with higher prey availability, and move straightforward in areas with less resources (Sims et al. 2008, Humphries et al. 2010). Therefore, studies of long trajectories performed by marine vertebrates often involve two types of movement behaviour (Barceló 2011):

i. Movement consistent with foraging behaviour, which happens when an animal presents slower surface speeds and increasing turning rates (this adaptive response to prey density is generally referred to as Area-restricted search (ARS) behaviour) (Block et al. 2011, Sommerfeld et al. 2013).
ii. Movement representative of transit (hence, not foraging), characterised by more directed movement with higher speeds and lower turning rates (Barceló 2011).

By definition, ARS is an indication of elevated search effort and it is possibly correlated with prey abundance (Robinson et al. 2007). According to Fauchald and Tveraa (2003) a predator searches for prey items within a patch of high prey density. To encounter as many prey items as possible per unit time, the predator should move fast and in straight lines. However, if the predator does not respond to the edges of the patch, such a fast, linear path will reduce the time spent within that patch. Thus, to increase the total time spent within the high-density patch, the predator should have a high turning rate and a low speed. Therefore, ARS is defined as increases in turning rate and decreases in movement speed where resources are plentiful (Fauchald and Tveraa 2003, Pinaud and Weimerskirch 2005, Jonsen et al. 2013) and is a common measure used to infer areas where animals are presumably presenting foraging behaviour. Many researchers use the identification of ARS-like behaviour to infer increased feeding activity (Boyd et al. 1998, Bradshaw et al. 2003, Robinson et al. 2007). ARS has been investigated using a number of simple analytical tools based on animal movement. Most of these methods assign an ARS index to every point along the track using

variables based on transit rate, turning rate, or residency. These variables are then averaged over some window of time or distance and a threshold is established to distinguish feeding from non-feeding behaviour (McConnell et al. 1999, Le Boeuf et al. 2000, Robinson et al. 2007).

Some authors mention that the use of ARS alone to designate foraging behaviour may not be entirely reliable. For instance, Sommerfeld et al. (2013), refer that, in a study with Southern elephant seals, foraging success was also observed when individuals were in transit. Outside these ARS zones, animals moved quickly through areas without slowing down or increasing their turning rate. This pattern has also been observed in other species, grey seals (Austin et al. 2006), basking sharks (Sims et al. 2006), suggesting that successful foraging without the adoption of ARS behaviour could be a common foraging method in marine predators. However, (Sommerfeld et al. 2013) also refer that ARS behaviour is related to enhanced diving activity and may be used as a proxy to identify important feeding areas for several species. Although foraging may occur without the adoption of ARS behaviour, it appears clear that foraging occurs with great intensity when they do adopt ARS behaviour. Therefore, identifying ARS behaviour has been central to understand how animals move through the environment in an effort to optimise their foraging success (Sommerfeld et al. 2013).

There is a need to better recognise how large marine vertebrates in the ocean make adjustments in their movements in response to food source patchiness (Pinaud and Weimerskirch 2005). Understanding their foraging behaviour and habitat characteristics will help to identify which should be main areas of conservation for endangered species (and there is an urgent need to identify these key marine areas, particularly in the high seas (Tancell et al. 2013). Documenting animal movements is, then, crucial for understanding species' home ranges, migration patterns, resource tracking, which is vital for predicting their responses to changes in the marine environment and for developing realistic conservation plans for marine species and their habitats (Boyd and Brightsmith 2013, Sommerfeld et al. 2013).

1.2 – Satellite Tracking:

The ability to answer questions regarding the behaviour of marine vertebrates in the open ocean has greatly increased with the latest advancements in technology, as is evidenced by the vast array of satellite telemetry tags available (Barceló 2011). Satellite tags have been used to track the movement of sea turtles since the 1980s, with an exponential increase in the number of studies and turtles tagged in recent years (Godley et al. 2008). These techniques have rapidly improved our knowledge on many aspects of sea turtles movements and

distribution (even with restrictions on the number of tracked turtles), such as the whole range of a population including nesting and foraging grounds, migration routes, home ranges, seasonal patterns, habitat use and navigational capabilities (Casale et al. 2012). These advances in satellite-mediated tagging technology coupled with a higher accessibility to many remotely sensed environmental data products, allow much more information to be currently available, in relation to location and movement of individuals and their exposure to a wide variety of environmental variables (Hays 2008).

There are several tracking instruments available for ecology studies in marine animals using telemetry systems, such as ARGOS (Advanced Research and Global Observation Satellite) system, best suited for animals that regularly spend time at the surface, Fastloc® GPS system, for studies where the animal's surfacing behaviour does not allow for quality ARGOS locations or when higher accuracy GPS quality locations are required, or light-based geolocation, more suitable for large pelagic movements of species that do not surface (Wildlife Computers, 2014). Many tags that have one of these systems incorporated also record and store useful environmental data, like temperature, salinity, and depth of the water where the tagged animals swim (Wildlife Computers, 2014). Other devices being deployed have the ability to measure feeding attempts and flipper or fin beats (i.e. swimming effort) on animals as diverse as spermwhales, seals and turtles (Wilson et al. 2002, Hays et al. 2004, Austin et al. 2006, Watwood et al. 2006). More recently, data loggers have been developed to directly record whether the turtle is sleeping or awake (Hochscheid et al. 2005), by attaching a motion sensor to the mouth of captive loggerhead turtles and measuring rhythmic movement of the throat region. There is an increasing use of advanced data loggers to extract information from different dive types, with even more linkage between what can be recorded by data-loggers and what can be relayed remotely (e.g. via satellite) (Hays 2008).

Beside satellite tracking and data-loggers, other methodologies have also been applied in marine ecology studies, with distinct or complementary purposes. Stable isotopes analysis (SIA) allows, for example, to establish a trophic relationship between species. This method has been applied in several trophic ecology and physiology studies of marine turtles (Godley et al. 1998, Wallace et al. 2006, Reich et al. 2007). Other techniques, like molecular tools, have also been used to assess small scale fidelity of both male and female turtles to particular nesting beaches (Lee et al. 2007), patterns of multiple paternity both within and across populations (Moore and Ball Jr 2002, Lee and Hays 2004, Jensen et al. 2006) and the links between the occurrence of juvenile turtles on foraging grounds and potential source rookeries (Bowen et al. 2005, Bass et al. 2006).

1.2.1 - ARGOS transmitters:

ARGOS transmitters have been widely applied in marine ecology studies. In fact, a great amount of distribution data for large, highly motile marine animals have been collected via ARGOS in the past decade (Godley et al. 2008, Hart et al. 2010, Arendt et al. 2012b), and these tracking devices continue to play an important role as scientists uncover more aspects of marine vertebrates' life in the oceans. A large portion of this global satellite telemetry data set is derived from loggerhead sea turtles (*Caretta caretta*) in the Northern Hemisphere (Godley et al. 2008). ARGOS is a satellite-based location and data collection system dedicated to studying the environment, developed as a result of French-American cooperation involving CNES (French Space Agency), NOAA (National Oceanic and Atmospheric Administration) [with support from NASA (National Aeronautics and Space Administration)], Eumetsat (European meteorological organization), ISRO (Indian Space Research Organization) and CLS (Collecte Localisation Satellites), operator of the system (ARGOS 2014). It allows any mobile object equipped with a compatible transmitter to be located across the world and also offers the possibility of collecting data from measurement sensors connected to this transmitter. When the tagged animals reach the surface of the water and are within the range of low-earth-orbit NOAA satellites (these satellites are at 850 km altitudes and each one simultaneously records all transmitters within an approximate 5000 km diameter "footprint", or visibility circle) (ARGOS 1996), transmitters deployed on the animals (PTTs - Platform Transmitter Terminals) automatically send a signal, termed as uplink, to the satellite (this occurs typically at an interval between 90 and 200 s) (ARGOS 2014). These signals are then transmitted from the satellite to a ground station that forwards the data to the ARGOS processing center (Jonsen et al. 2005). ARGOS centers calculate a transmitter's location using the Doppler shift on transmission frequency on a single overpass (Hays et al. 2001) (a pass generally lasts for 10 minutes) (Jonsen et al. 2005). The Doppler shift is the change in frequency of a sound wave or electromagnetic wave that occurs when the source of vibration and observer are moving relative to each other (when the satellite approaches a transmitter, the frequency of the transmitted signal measured by the on-board receiver is higher than the actual transmitted frequency, and lower when it moves away) (ARGOS 1996). Each time the satellite receives a message from a transmitter, it measures the frequency and time-tags the arrival. A major feature of the Doppler location is the existence of two symmetrical possible positions of the platform that give exactly the same frequency measurements on board the satellite: the nominal ("true") location and the mirror ("virtual") location. For each of the two possible locations, and by using all messages received during the satellite pass over the platform, a least-squares analysis is used to refine the estimates of the transmitter's position.

An estimation of the location accuracy is calculated using the residual error and the satellite pass characteristics. According to ARGOS, precision varies, and locations are divided into quality classes, that assign a level of accuracy to each location, based generally on the number of uplinks from transmitter to satellite, the time between these uplinks, and the time since a previous location was estimated (Austin et al. 2003). When more than three uplinks are available, a quality location class (LC) is computed (LC 0, 1, 2 or 3), while LC A is given when only three uplinks are available and the LC B is given when only two uplinks are available. The lower the number of uplinks, the more uncertain is the location accuracy (Bailleul et al. 2007). Error is assumed to be isotropic and hence characterised by a single number called the radius of error and it corresponds to one standard deviation (sigma) of the estimated location error. The location class is attributed based on the radius of error (ARGOS 2014), as described in TABLE 1.

TABLE 1 - ARGOS Location Classes (LC) and respective estimated errors.

LC	Estimated error	uplinks
3	< 250 m	> 3
2	250 - 500 m	> 3
1	550 -1500 m	> 3
0	> 1500 m	> 3
A	No accuracy estimation	3
B	No accuracy estimation	2
Z	Invalid location	-

Although ARGOS provides a level of accuracy for each location class, some authors (Hays et al. 2001, Bradshaw et al. 2007) have been independently accessing location quality in the past few years. Hays et al. (2001) refer that LC 3, 2 and 1 accuracies correspond approximately to those provided by ARGOS. However, accuracy of LC A was comparable to that of LC 1, LC B had poorer accuracy than LC A and the worst level of accuracy was found in LC 0, with location errors on the order of 10 km. Failure to account for large errors relative to the scale of movement can result in large biases in the interpretation of optimality in foraging dynamics and searching behaviour (Bradshaw et al. 2007). So, even if relevant biological information can be acquired from relatively noisy data, it is extremely important to have in consideration the associated errors and the scales at which they occur.

1.3 – Sea turtles

Sea turtles are long-lived and slow-growing animals that mature late and spend almost their entire life at sea (TEWG, 2009). Being reptiles, these animals are largely considered to be

ectothermic and, consequently, to have a low metabolic rate, which enables them to survive for very long periods of fasting associated with long distance migrations (Hays 2008). They move great distances during their lifetimes, while migrating between foraging and nesting grounds. In fact, they are the only reptiles known to migrate long distances between breeding and foraging sites (Schofield et al. 2010b).

After spending several decades in the sea, mature turtles mate in near-shore waters (Davenport 1997) and females return to nesting beaches to lay their eggs. As soon as they are born, hatchlings emerge and head to the ocean, where they will spend a large portion of their life, moving in and out of a variety of ocean and coastal habitats (Conant et al. 2009).

Sea turtles exist for more than 100 million years and represent an ancient and distinctive part of the world's biological diversity. Although they were abundant in the 18th and 19th centuries (with some populations reaching over millions of individuals), these animals now struggle against extinction, as humans overcome their ability to maintain the populations' numbers, by intentional and accidental capture in fisheries, destruction of foraging, nesting and resting habitats, and, most recently, climate changes and pollution of the oceans (NMFS 2013).

There are currently seven sea turtles species clearly recognized - green turtle (*Chelonia mydas*, Linnaeus 1758), loggerhead (*Caretta caretta*, Linnaeus 1758), flatback (*Natator depressus*, Garman 1880), hawksbill (*Eretmochelys imbricate*, Linnaeus 1766), leatherback (*Dermochelys coriacea*, Vandelli 1761), olive ridley (*Lepidochelys olivacea*, Eschscholtz 1829), and Kemp's ridley (*Lepidochelys kempi*, Garman 1880). Many scientists also consider the distinctive 'black' turtles of the Pacific coast of the Western Hemisphere, sometimes referred to as *Chelonia agassizi* (Bocourt, 1868) as an eighth species (NMFS 2013).

Most species have circumglobal and subtropical or tropical distributions (COSEWIC 2010) and may undertake long journeys between natal and foraging areas, and even between different foraging locations (Monzón-Argüello et al. 2009). All species (except the Australian flatback) are listed in the IUCN Red List as Endangered or Vulnerable (IUCN, 2014) and included in Appendix I of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora), and all species except the flatback are listed in Appendices of CMS (Convention on the Conservation of Migratory Species of Wild Animals) (Conant et al. 2009).

Although marine turtles spend the majority of their time at the sea, management and conservation programs all over the world mainly focus on nesting beach activities, which has resulted in little information about a large portion of these animals life time (COSEWIC 2010). A reason for that lack of knowledge is related to the fact that monitoring animals in their oceanic life stages is quite challenging, and only about two decades ago advances in technology have allowed to go deeper in studies about marine vertebrates at sea (Hays 2008).

In fact, improvements in telemetry techniques in these past few years have greatly contributed for a better understanding of sea turtles activities in the oceans (e.g. migrations extension, foraging grounds, juvenile “lost years”). However, there are still current difficulties in detecting migration patterns and foraging grounds, since an oriented migration survey would require to know when a turtle will make this journey, as well as capturing such turtles for instrument attachment (Hays 2008). The temporal and spatial scales over which marine turtle life histories occur also makes it difficult to undertake comprehensive ecological studies (Rees et al. 2013).

Marine turtles serve important functions in the ecosystems in which they are found (although details of those functions may be hard to clarify, as populations currently face serious depletion). Seagrass beds where green turtles graze regularly are more productive, nutrients are cycled more rapidly, and the grass blades have a higher protein content, thus benefiting other species (Conant et al. 2009). Some populations of marine turtles, whose foraging areas may be thousands of kilometres from their nesting beaches, serve an important role in nutrient cycling, as they carry large quantities of nutrients from these feeding grounds to their nesting beaches that are typically more nutrient-poor coastal and inshore habitats (Conant et al. 2009).

It is widely recognised that sea turtle conservation cannot be limited to the reproductive phase and sites, but requires measures oriented to also protect turtles of all stages in their foraging grounds (Casale et al. 2012). Long-term monitoring of populations is revealing conservation concerns as well as conservation success stories (Hays 2008), and key remaining issues related to the biology and conservation of this group are now starting to become more clear.

1.4 – Loggerhead turtle

This species was first described by Linnaeus in 1758 and named *Testudo caretta*. Over the next two centuries more than 35 names were applied, but there is now agreement on *Caretta caretta* as the consensual name (Conant et al. 2009).

1.4.1 - Distribution and habitat:

The loggerhead sea turtle inhabits all tropical and temperate ocean basins, and has a life history that involves nesting on coastal beaches and foraging in neritic and oceanic habitats, as well as long-distance migrations between these areas. The majority of loggerheads nesting sites is at the western rims of the Atlantic and Indian Oceans. Recent reviews show that only

two loggerhead nesting aggregations have more than 10000 females nesting per year: Peninsular Florida (United States) and Masirah Island (Oman) (Conant et al. 2009). Other nesting spots with considerable number of females nesting (above 1000 females nesting annually) may be found in Mexico, Brazil, Cape Verde, Australia and Japan, as other countries possess smaller nesting aggregations (Dry Tortugas (U.S.), Cay Sal Bank (The Bahamas), Tongaland (South Africa), Mozambique, Arabian Sea Coast (Oman), Halaniyat Islands (Oman), Cyprus, Greece, Turkey and Queensland (Australia) (COSEWIC 2010). In the eastern Atlantic, the largest nesting population of loggerheads is in the Cape Verde Islands (L.F. López- Jurado, personal communication, cited in Ehrhart et al. 2003), and some nesting occurs along the West African coast (Conant et al. 2009). At the present moment, there are no data on population size in the oceanic habitat (Conant et al. 2009).

1.4.2 - Atlantic Ocean loggerheads:

The Northwest Atlantic Ocean loggerhead turtles, hatched in the U.S beaches, enter the ocean, swim to leave the waters of the continental shelf, and become entrained in the Gulf Stream (TEWG, 2009). They are carried by the North Atlantic gyre to Northeast Atlantic waters of the Azores, Madeira and the Canary Islands (Monzón-Argüello et al. 2009). These juveniles are also found in the Mediterranean Sea (Carreras et al. 2006, Eckert et al. 2008). In these areas, these migrating animals overlap with animals originated from the Northeast Atlantic and the Mediterranean Sea (Conant et al. 2009).

Monzón-Argüello et al. (2009) refers that migrating juvenile turtles do not distribute randomly, providing some evidence that juveniles distribute in order to forage in areas of similar latitude to their original rookery. Southern rookeries, such as Mexican population, prefer southern latitudes to feed, while Northern populations, such as south Florida population, are more common in Azores than in Madeira or Canary Islands.

The North Atlantic oceanic juvenile stage has been primarily studied in the waters around Azores and Madeira (Bolten et al. 1998). Satellite telemetry data and flipper tag data obtained suggested a long period of residency in Azorean waters, but in waters around Madeira, turtles appear to be only passing through (Conant et al. 2009).

In the Northeast Atlantic, satellite telemetry studies of post-nesting females from Cape Verde identified two distinct dispersal patterns: smaller individuals foraged primarily oceanically off the northwest Africa coast and larger individuals migrated to benthic foraging areas off the northwest Africa coast (Hawkes et al. 2006). Monzón-Argüello et al. (2009) conducted a mixed stock analysis of juvenile loggerheads sampled from foraging areas in the Canary Islands, Madeira, Azores, and Andalusia and concluded that juveniles from the Cape

Verde population were distributed among these four sites (although a large proportion of Cape Verde juveniles appear to inhabit as yet unidentified foraging areas).

1.4.3 - Biology:

The loggerhead turtle (FIGURE 1) is perhaps the best researched marine turtle species, with most studies of loggerhead growth and life history traits concentrated on the nesting population along the southeast coast of the USA, in the Western Atlantic Ocean (Davenport 1997). This species presents a reddish-brown carapace, both in juveniles and adults, often described as heart-shaped, usually five pairs of costal scutes (COSEWIC, 2010). The dorsal and lateral head scales and the dorsal scales of the flippers are also reddish-brown, but with light to medium yellow margins. The plastron is medium to light yellow. Hatchlings vary from light to dark brown to dark grey dorsally and lack the reddish-brown coloration of adults and juveniles (Conant et al. 2009).

FIGURE 1 - Juvenile loggerhead turtle (source: *http://galeri8.uludagsozluk.com/422/caretta-caretta_535827.jpg*)

At emergence, hatchlings average 45 mm in SCL (straight carapace length) and weigh approximately 20 g (Conant et al. 2009).

Recorded carapace lengths for loggerheads have exceeded 210 cm, with weights above 450 kg, but the average mean carapace length of nesting loggerheads in the Atlantic is 94 cm, and the mean body mass of females is 116 kg (COSEWIC 2010).

Although in earlier stages there are no distinctive morphological characteristics between males and females, sexual dimorphism is usually apparent in individuals with more than 67 cm SCL (Dodd 1988). The most easily identifiable differences are tail length and claws (Wibbles 1999). As with other sea turtles, male loggerheads have a longer, thicker and more muscular tail than do females (Dodd 1988; Wibbles 1999). The male turtle's tail extends well beyond the carapace, while the tail of the female turtle barely extends beyond it (Wibbles 1999). Although both male and female have claws on their front flippers, males have a claw on each flipper that is conspicuously larger and more strongly curved than the rest (COSEWIC 2010).

There is uncertainty on the age of maturity of loggerheads, but estimates range between at least 10 and 45 years (Abecassis et al. 2013). Loggerheads nest on ocean beaches and occasionally on estuarine shorelines. Nests are typically laid between the high tide line and the dune front (Conant et al. 2009), in wide, sandy beaches backed by low dunes and fronted by a flat, sandy approach from the water. Mature female Loggerheads return to land only to nest. They nest on a 2-3-year interval. The sex of hatchlings is temperature dependent. Incubation temperatures above 29°C produce more or all females, and incubation temperatures below 29°C produce more or all males (COSEWIC 2010).

This species is known to inhabit all tropical and temperate ocean basins, and may be found in wide-ranging temperatures (10.1 - 29.7 °C) (Casale et al. 2012), although their optimal preference is thought to be around 17°C (Abecassis et al. 2013). According to Polovina et al. (2004), loggerheads spend about 40% of their time near or at the surface, and about 90% of their time at depths <40 m, also exhibiting relatively shallow dives. Howell et al. (2010) also mention the epipelagic habitat of these turtles, referring that they spend 90% of their time within the first 5 m of the water column. Foraging home range areas of adult loggerhead turtles have been demonstrated to be as large as 10 km^2 in neritic habitats and up to 1900 km^2 in oceanic habitats (Schofield et al. 2010c, Hawkes et al. 2011). Loggerheads' average swimming speeds are variable. For reference purposes, (Polovina et al. 2000) mention swimming speeds ranges from about 24–32 cm/s, while Abecassis et al. (2013) refer speeds under 1 km/h (28 cm/s) and increasing with size. These animals are known to perform some of the greatest distances within their migrations, with records of thousands of kilometres travelled during these journeys (e.g. over 6000 Km (Mencacci et al. 2010) and traversing both major ocean basins (Kobayashi et al. 2008).

1.4.4 - Life cycle:

Immediately after emerge from their nests, the hatchlings begin a period of frenzied activity, as they move from their nest to the surf, swim, and are swept through the surf zone (Conant et al. 2009). As post-hatchlings, loggerheads are pelagic and inhabit neritic waters along the continental shelf. This stage lasts for weeks or months (Witherington 2002), until they grow and are carried within ocean currents (Bolten et al. 1998), beginning the oceanic stage. The oceanic juvenile stage lasts for several years that are usually referred to as “the lost years”, since until recent years it was not confirmed where these juveniles would remain for around the first years of their lives. They would leave the beaches where they were born, with a size of approximately 45 mm (Wallace et al. 2009), only returning after a decade or more, with the size of a dish (about 46 - 64 cm CCL). In this stage, it is now known that these juveniles move with the predominant ocean gyres, before returning to their neritic foraging and nesting habitats (Conant et al. 2009). In the Atlantic Ocean, turtles that are born in the east coast of the United States spend approximately the first decade of their lives inhabiting the North Atlantic Gyre (a circular current system that encircles the Sargasso Sea) (Avens et al. 2003). Although it was thought that these pelagic juveniles would mostly be drifting with the oceanic currents, recent studies (Polovina et al. 2004) revealed that, despite their small sizes, these turtles are active swimmers. In fact, even post hatching loggerheads have well-developed swimming skills (Kobayashi et al. 2008). These juveniles are probably opportunistic drifters, using the currents as it is more profitable for them to forage, and have been characterised as “smart” drifters, with alternating periods of passive floating and directed swimming based on suitability of forage and habitat (Conant et al. 2009).

In the Atlantic, (Bjorndal et al. 2000) estimated oceanic juvenile stage to be between 7 and 11.5 years, with juveniles recruiting to neritic habitats in the western Atlantic over a size range of 46-64 cm CCL, although other authors (Snover et al. 2007) suggest a much longer oceanic juvenile stage duration within a range of 9-24 years.

The neritic juvenile stage begins when loggerheads gradually exit the oceanic zone and recruit the neritic foraging areas, often returning to the coast of the beaches where they were born (Avens et al. 2003). Experimental displacements have shown that these animals have navigational abilities based, at least in part, on magnetic information (Monzón-Argüello et al. 2009). In Western Atlantic, these juveniles exhibit a size range of 46-64 cm curved carapace length (CCL) (TEWG, 2009), although in other places, these sizes may vary (60 cm SCL in Japan (Y. Matsuzawa and Sea Turtle Association of Japan, unpublished data, *in* COSEWIC 2010), 70 cm CCL or larger in Australia (Limpus et al. 1994 *in* Conant et al. 2009) and 25 cm CCL (P et al. 2008) in the Mediterranean). After migrating to the neritic zone, juvenile

loggerheads remain in these habitats for roughly 20 years (Wallace et al. 2009) where they continue maturing until they reach adulthood at a minimum size of around 87 cm SCL. However, both juveniles and adults may periodically move between the neritic and oceanic zones (Conant et al. 2009). The neritic zone also provides important foraging habitat, inter-nesting habitat, and migratory habitat for adult loggerheads (COSEWIC 2010).

The duration of the adult stage can be reasonably estimated for females from tag return data at nesting beaches. For the Northwest Atlantic nesting assemblages, data show reproductive longevity, and hence duration of adult female stage as long as 25 years (TEWG 2009). This is likely an underestimate of the average reproductive life span given tag loss and incomplete surveys of nesting beaches at night (Conant et al. 2009). Turtles recruiting this stage in the Northwest Atlantic have about 82 cm SCL, with full recruitment to the adult stage occurring at 100 cm SCL (TEWG 2009). Genetic sequencing confirms that adult female loggerheads present “natal homing,” returning to the vicinity of their natal beaches for mating and nesting (Bowen and Karl 2007). Loggerheads from different populations often mix in common foraging grounds (Bolten et al. 1998), which creates difficulties when attempting to delineate distinct population segments for management or listing purposes.

1.4.5 - Diet composition:

Loggerheads feed opportunistically on many types of invertebrates (Avens et al. 2003), and their diet vary with their prey availability between oceanic and neritic (or coastal) sites (Schofield et al. 2010b).

After hatching, small juvenile loggerheads spend more than a decade in the epi-pelagic zone amongst floating *Sargassum*, feeding opportunistically on nektonic organisms (McClellan et al. 2010). Studies in the North Pacific Ocean (Polovina et al. 2004) revealed that loggerheads most common prey in oceanic grounds are floating organisms and organisms riding on floating objects. These include the predatory gastropod *Janthina sp*. and its prey *Vellela vellela* (By-the-wind sailor), gooseneck barnacles, *Lepas sp*., and the pelagic crab *Planes cyaneus*, which ride on logs, floats and often *V. vellela*.

As large juveniles, these turtles return to neritic waters and adopt a demersal foraging strategy, feeding on benthic invertebrates, including crustaceans and molluscs. During this developmental period, the turtles undergo morphometric and physiological changes that are consistent with changes in their foraging ecology (McClellan et al. 2010). Populations from different geographic locations forage on different kinds of prey, which makes the list of the types of prey eaten by loggerheads in the wild extensive (Plotkin et al. 1993).

Loggerheads are also known to ingest other items that occur in the water column but do not constitute typical loggerhead prey, such as anthropogenic debris and discarded fish and shrimp, reflecting their opportunistic, generalist foraging strategy (Wallace et al. 2009).

Seney and Musick (2007) (Wallace et al. 2009) reported a long-term temporal shift in diet composition in loggerheads in Chesapeake Bay, USA, based on stomach content analyses. Loggerheads diets consisted mainly of horseshoe crabs (*Limulus polyphemus*) in the 1970s, blue crabs (*Callinectes sapidus*) in the 1980s, and fish in the 1990s. These changes probably reflected dietary supplementation with fishery discards due to the decline in their typical prey items.

1.4.6 - Environmental key variables:

Foraging is probably the primary determinant of loggerhead pelagic habitat selection (Kobayashi et al. 2008). Some authors (Polovina et al. 2004, Kobayashi et al. 2008) have documented the relationship between some physical and biological ocean characteristics and foraging behaviour of many predators. Two environmental ocean variables have been shown to have great association with foraging grounds selected by loggerhead turtles: sea surface temperature (SST) and chlorophyll *a* concentration (Chl*a*) (Polovina et al. 2000, Kobayashi et al. 2008). Sea surface temperature (SST) is known to be a strong orientation cue for sea turtles (McMahon and Hays 2006, Kobayashi et al. 2008). Seasonal migrations between high latitude foraging grounds and lower latitude overwintering areas have shown to be temperature-linked (Davenport 1997). It has been observed in some loggerhead population and areas, like the north-western Atlantic, that turtles migrate to remain in waters above 17°C (Hawkes et al. 2011, Casale et al. 2012). This fact has also been corroborated by Barceló (2011), who mentioned that the turtles' movements in his study, when summarized for latitude by season, corresponded closely with the seasonal variability in SST. The importance of SST indicates that preferred habitat may be seriously affected by trends in ocean temperature, for example El Niño Southern Oscillation events, climate change, or global warming may reposition migratory pathways, and possibly remap critical intersections with high-seas fisheries (Kobayashi et al. 2008).

According to Polovina et al. (2001), chlorophyll *a* is likely a key variable for pelagic habitat since it may suggest forage availability for loggerhead sea turtles. The presence of chlorophyll *a* is indicative of the existence of phytoplankton, which allows a trophic cascade to occur (from zooplankton feeding on phytoplankton to top predators feeding on other species). In the North Pacific, a relationship between loggerheads' habitat and a preferred range of surface chlorophyll *a* has been identified (0.1–0.3 mg/m3) (Polovina et al. 2001). This range

corresponds to the Transition Zone Chlorophyll Front (TZCF), a basinwide surface chlorophyll *a* front that represents the boundary between the high surface chlorophyll *a* concentrations of the Subarctic Gyre and the low concentrations of the North Pacific and was considered an important loggerhead sea turtle foraging habitat, as it is thought to represent a zone of surface convergence that would concentrate the buoyant, surface prey of loggerheads (Polovina et al. 2001, Parker et al. 2005).

Loggerheads are also found in association with other oceanographic features, such as low bathymetry regions, thermal fronts, eddies, and geostrophic currents. Sea turtles are highly dependable of oceanic currents, both in their earlier years, as in migrations throughout the oceans, between foraging and nesting grounds (Polovina et al. 2004). Recent studies (Polovina et al. 2006) revealed that loggerheads use a variety of features including cyclonic and anti-cyclonic eddies, and meanders, as upwelling occurring in these formations provide foraging habitat for many trophic levels. Although many hot-spots are patchy and temporary (e.g., open-ocean eddies or small-scale fronts), physical features that are relatively fixed spatially or that persist through time may be more ecologically relevant, as they may lead to food chain development and trophic interactions from primary producers up to the highly mobile nekton (Palacios et al. 2006). Processes that occur on regular cycles (e.g., seasonal coastal upwelling in eastern boundary current systems) may also be very significant, as they may lead to the predictable development of exploitable foraging regions year after year, and many marine species have evolved to synchronize their life cycles with the presence of these persistent and repeatable features (Cushing 1990).

1.4.7 - Conservation status:

Loggerhead turtle is listed by IUCN as endangered over its entire distribution range (IUCN 2013), and has been, since 1996, listed in CITES (*Convention on International Trade in Endangered Species of Wild Fauna and Flora)* Appendix I (IUCN 2013). Despite almost 20 years have gone by since these animals have been considered in need of serious conservation measures, loggerheads still face several anthropogenic threats, at every stage of their life cycle, such as loss of nesting beaches, directed takes, ingestion of marine debris, environmental contamination, diseases, and interactions with various fisheries (pound net, gillnet, trawl and longline fisheries) (Abecassis et al. 2013).

Although fisheries interactions and coastal development have been identified as the threats causing most concern (Rees et al. 2013), climate changes may also be playing a very important role in the decreasing number of individuals of sea turtles' populations, with profound impacts, such as altering the timing of the nesting season, species distributions (Hays 2008),

migration routes (as changes occur in oceanic currents' patterns) (Davenport 1997), as well as in sex-ratio of the hatchlings, as higher temperatures will possibly favour the development of female hatchlings (Davenport 1997). Long-term data-sets will be increasingly important in detecting these and other possible changes.

Although marine turtles spend most of their lives in the open ocean, between foraging and nesting grounds, or in migration processes, most of the conservation efforts have been taken in nesting sites. If, by one hand, assessing habitat characteristics in the ocean is more challenging than on nesting sites, on the other hand, increasing technologies continue to reveal more about these animals' ecology during migrations and while foraging. Satellite telemetry is proving to be a useful tool for that purpose (Peckham et al. 2007, AC et al. 2012, Boyd and Brightsmith 2013), although long-term studies are needed to accurately assess migratory routes, habitat use and most frequented areas (M et al. 2010), to support efficacy of conservation measures in these long-lived species (Rees et al. 2013). Although there have been recently more studies related to ocean turtles' habitats, the majority of them focus in the Western Atlantic (Avens et al. 2003, Arendt et al. 2012a), the North Pacific (Polovina et al. 2004, Kobayashi et al. 2008, Abecassis et al. 2013), some in the Mediterranean (Bentivegna 2002, Mazaris et al. 2009, Monzón-Argüello et al. 2009, Luschi et al. 2013), and in the Eastern Atlantic (Monzón-Argüello et al. 2009, McCarthy et al. 2010). As a highly migratory species, loggerhead turtles and their widespread habitats have to be seen as a whole, which means that both ecology studies and conservation efforts should be considered as a worldwide process.

1.5 - Objectives

This work aims to identify foraging habitats of North-Atlantic juvenile loggerhead sea turtle (*Caretta caretta*), by determining area-restricted search with a combination of three commonly used methods, and understand which environmental variables are related to these animals' preferences for foraging. Other features, related to the turtles' paths, will also be investigated, such as latitude ranging variability by seasons and possible currents interactions with the animals' trajectories. The obtained results in this work will integrate a larger ongoing study related with many aspects of sunfish (*Mola mola*) foraging habits.

2 - METHODS

2.1 – ARGOS data collection and filtering:

2.1.1 - Tagging procedures:

The analysed data were obtained in the years of 1998 and 1999, by Dellinger et al.
ARGOS satellite transmitters (Wildlife Computers - model SDR-T10) (Dellinger and Freitas, 1999 *in* McCarthy et al. (2010) were deployed in 10 juvenile loggerhead turtles, in Madeira (Portugal), in spring (5 animals tagged in April and May) and autumn (5 animals tagged in September), in the year of 1998. The animals were hand captured from a boat off the south coast of Madeira and brought to land. Tags were attached as backpacks, during captivity, as followed by Balazs et al. (1996) and the turtles were released from boats about a week after capture (7.6 ± 2.7 days) (McCarthy et al. 2010). Data were recorded until the tags stop transmitting (which would be for the entire life of the animal or the transmitter) (Dellinger and Freitas, 1999) in McCarthy et al. (2010).

2.1.2 - Remove invalid locations (LCZ) and check outliers' coordinates:

Because raw ARGOS-derived data contained all locations, despite their quality classes, a post-processing of locations was necessary. The first step was to discard all LCZ locations, as these are invalid locations (see 1.2.1). 386 locations were removed from a total of 9190 locations (see TABLE 2). Due to the Doppler Effect (see 1.2.1), two possible locations are provided by the ARGOS system for each point (the true location and its mirror image). The algorithm which chooses the true location between them may sometimes fail (Bailleul et al. 2007), therefore the second step was to confirm if any of the outliers was under this possible failure. So, for all the outliers, a visual confirmation of their coordinates was made, by plotting the tracks in ArcMap™ (ESRI 2011) and checking if the second set of coordinates was closer than the first to the animal's path (having in consideration the previous and following positions). Whenever it did, this set of coordinates was assumed to be the correct one.

TABLE 2 - Quality class "Z" (LCZ) locations for each track.

Track	LCZ	Total number of locations
12007	42	1055
12538	37	717
12544	43	1439
12545	34	1244
12546	15	638
12547	59	1077
12570	61	1195
12571	56	1085
12573	24	560
12574	15	180
TOTAL	**386**	**9190**

2.1.3 - Tracks smoothing and standardising (SSM-KF):

ARGOS raw data consist in a series of locations observed through time, with a quality class assign to each one (see 1.2.1). Estimation errors, associated with these quality classes, vary through time and are strongly non-Gaussian (Jonsen et al. 2005). Moreover, ARGOS observations occur irregularly over time, producing an artificial perspective on the animals' movement process (Jonsen et al. 2005). For these reasons, it is necessary to apply some filtering to the data. Filtering methods often consider only locations with quality classes of, 0, 1, 2 or 3. However, many locations in ARGOS raw data have A or B quality classes, and eliminating these locations would largely reduce the amount of information that could be obtained from the original tracks. In this work, a State Space Model (SSM) that uses the Kalman-filter (KF) was applied to the data, in order to smooth the path and standardise the observations in time. SSM are time-series methods that allow unobserved states and biological parameters to be estimated from data observed with error (Jonsen et al. 2005). They account for the fact that true movement is observed neither continuously, nor with complete accuracy (Schick et al. 2008). The filtering process provides a valuable tool for modelling movement data by simultaneously accounting for measurement error and variability in the movement dynamics (Bailey et al. 2008). The selected SSM was fitted to the data using R software (R Development Core Team 2011), package CRAWL (Correlated Random Walk Library) (Johnson 2013). Models using Correlated random walks (CRWs) involve a correlation between successive step orientations, meaning that instead of a "walker" being able to move

from its current positon in any independent direction (therefore, having no relation with the direction of its previous positions, which is the case in a simple random walk), in CRWs, each step tends to point in the same direction as the previous one, although the influence of the initial direction of motion progressively diminishes over time and step orientations are uniformly distributed in the long term (Codling et al. 2008). Since most animals have a tendency to move forward, CRWs have been widely used to model animal paths in various contexts (Codling et al. 2008). R package CRAWL (Johnson 2013) was designed for fitting continuous-time correlated random walk (CTCRW) models with time indexed covariates and the model is fit using the Kalman-Filter on a state space version of the continuous-time stochastic movement process (Johnson 2013). The Kalman filter is a mathematical method named after Rudolf E. Kalman and its purpose is to use measurements that are observed over time and contain noise (random variations) and other inaccuracies, and produce estimates of the true values of measurements and their associated calculated values by predicting a value, estimating the uncertainty of the predicted value, and computing a weighted average of the predicted value and the measured value. The most weight is given to the value with the least uncertainty. The estimates produced by this method tend to be closer to the true values than the original measurements because the weighted average has a better estimated uncertainty than either of the values that went into the weighted average (ARGOS 1996).

CRAWL (Johnson 2013) was chosen among other possibilities, because it has proven to have the least error, in relation to the GPS data (Queiroz and Sousa, unpublished data). This method allows all locations to be included, which represents a great advantage in relation to other filtering methods, because ARGOS tracks often have a large amount of low quality classes' locations (Table 3).

TABLE 3 - Quality classes frequency for the 10 tracks. LC: locations' quality classes; Total: total number of locations that have that quality class; Freq – Frequency of that quality class (total number of that quality class divided by total number of locations)

LC	Total	Freq
0	1816	0.206
1	1815	0.206
2	972	0.110
3	318	0.036
A	1605	0.182
B	2278	0.259

First, errors (weights) are assigned to latitudes and longitudes, according to locations' quality classes. Then, the model is run to smooth the paths, by adjusting locations' coordinates

according to their weights and, finally, the track is regularized in time, by interpolating locations with a previously determined desired time-step. Since the minimum mean number of positions/day was less than 3 (2.95 positions/day, ID12574) (see Table 4), the time-step chosen to run the model was ½ (calculates a position every 12h), so that the result would have a conservative amount of 2 positions/day.

TABLE 4 - Summary information of raw data. Days: total number of days tracked; Posit/day: mean number of positions for day; Max gap (days): maximum number of days without any position.

ID	Days	Posit/day	Max gap (days)
12007	279	3.63	2.96
12538	158	4.31	2.10
12544	273	5.11	1.52
12545	277	4.36	2.57
12546	108	5.75	1.98
12547	342	2.98	3.54
12570	311	3.64	10.45
12571	340	3.03	3.84
12573	123	4.37	2.04
12574	56	2.95	2.59

2.1.4 - Remove inland positions:

The filtered tracks were plotted in ArcMap™ (ESRI 2011) and the coastline was added to the project, to better visualize the paths and remove possible inland locations from the tracks.

2.2 – Determining Area-restricted search (ARS):

There are several methods commonly used, solely or combined, to determine ARS behaviour, such as the moving average, first-passage time, residence time or fractal landscape (Knell and Codling 2012), among many others. Because every method has its unique technique to reveal foraging behaviour, by accounting for different behaviour characteristics (e.g. velocity of the animal, time spent in an area, tortuosity of the path, etc.), using only one method could mask other possible foraging sites that are not detectable by the change in that behaviour, or, by opposition, consider erroneous foraging areas, based on that one behavioural change. For those reasons, three different methods were applied and later combined to determine ARS:

first passage time (FPT), speed (corrected with ocean currents) and sinuosity of the path (straightness index). Details of each method and respective procedures are described below.

2.2.1 - First Passage Time:

First passage time (FPT) (Johnson et al. 1992) is defined as the time required for an animal to cross a virtual circle with a given radius. In the analysis, one centers a window of radius r on the origin of a random walker and records how long it takes the walker to leave this circle. This time is the mean first passage time. Fauchald and Tveraa (2003) extended this analysis by making the link between FPT and search behaviour in order to connect these movement patterns to landscape patterns. Their hypothesis was that organisms with higher FPT in certain areas would be exhibiting area-restricted search. The first step is to determine, along a track, the radius with higher FPT variance, as this will be the radius of a virtual circle size where the animal is theoretically spending more time (thus, supposedly foraging). The second step is to determine the animal's usage of this radius, by moving that virtual circle along the track. The estimated relative variance $\hat{S}_r$, in FPT is calculated as a function of r: $\hat{S}_r = \text{Var}[\log(t_r)]$, where t_r is the FPT for a circle of radius r (Bradshaw et al. 2007). This log transformation makes $\hat{S}r$ independent of the magnitude of the mean FPT (Fauchald and Tveraa 2003).

So, to determine FPT, for each track, a circle of the smallest considered radius (it was considered a minimum radius of 10000 m, as this is the maximum ARGOS error [see Hays et al. (2001)] was moved along the track at equidistant points by creating intermittent steps along each track, with this procedure repeated for circles of increasing radii (to detect the radius with higher activity). The increasing radii were calculated to a maximum of 400000 m (this maximum was chosen based on the first trials to determine FPT variance, as it was graphically visible that higher radii would no longer be representative of area-restricted search and also didn't enable a clear visualization of the peaks). A total of 300 radii were fitted between the two limits, meaning that each increasing radius had more 1300 m than the previous one. This analysis was then visualized in a graph, and the higher FPT variance radius, corresponding to the highest visualized peak, was the chosen radius, meaning that, theoretically, the circle with that radius is the scale the animal uses the most to forage. For each track, radii chosen to determine FPT are presented in TABLE 5.

The second step was to refine the search, moving the selected radius along the track length, to determine how the animal uses this "foraging scale" along its path. For each location, log (FPT) values were determined, for posterior ARS calculation. FPT analysis was performed in R (R Development Core Team 2011), using packages: rgdal (Bivand et al. 2013), ade4 (Dray and Dufour 2007), adehabitat (Calenge 2006) and argosfilter (Freitas 2012).

TABLE 5 - Radii with higher FPT variance for each track:

Turtle ID	FPT radius (m)
12007	100000
12538	100000
12544	25000
12545	50000
12546	50000
12547	50000
12570	200000
12571	100000
12573	50000
12574	50000

2.2.2 – Corrected velocities:

Animals' foraging behaviour is related to decreasing velocities along their paths, since in areas where resources are higher, it is expectable that the animal will decrease its speed for a more successful food exploitation. On the other hand, foraging typically occurs in rich, dynamic areas where currents tend to be faster. In such areas, the balance between oceanic movements and animal motion may be subtle (Gaspar et al. 2006). According to these authors, sea turtles' trajectories are greatly influenced by the oceans' currents, and neglecting them may affect several important results deduced from the analysis of tracking data, including the identification of foraging areas. The trajectories of marine animals reflect the combined effects of the animal's voluntary motion (swimming) and its transportation by oceanic currents (drift), which makes their velocity dependent on currents directions and magnitudes. So, to analyse and correct the animals' velocities, it is first necessary to know the currents velocity and direction at each location.

To obtain the currents directions and magnitudes, Global Delayed-time Updated Merged mean sea level anomalies (Global DT-Upd MSLA) produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes (http://www.aviso.oceanobs.com/duacs/) were used. These DT products provide a long term, more accurate time series. The parameters extracted were the currents direction (dir - Direction of geostrophic water flow, in degrees) and magnitude (mag - Absolute magnitude (or modulus) of the geostrophic water velocity vector, in cm/s), for the locations in the turtles' tracks. AVISO geostrophic currents are available in Mercator projection, with a nominal cell size of 1/3 degree, and these data were

interpolated at points at a weekly (7 days) time-step. Weekly images are not created by aggregating the daily products together (they are not produced taking mean of seven daily images, for example). They are just a sparse selection of the daily images (every seventh daily image exactly matches a weekly image, pixel for pixel).

These procedures were made using a free, open-source geoprocessing toolbox - Marine Geospatial Ecology Tools (MGET) (Roberts et al. 2010), and performed in ArcMap™ (ESRI 2011).

To determine the corrected velocities for each turtle, the animal speed (cm/s) at each location (distance of that location to the previous one divided by the elapsed time between them) was first calculated. Then, the direction of the turtle at each location was calculated and vectors were created for both directions and velocities of the turtle and the currents at each location. The absolute difference between directions of turtle and current was then calculated and, finally, the corrected speed is determined, using the cosine law: $c^2 = a^2 + b^2 - 2ab.\cos\gamma$ (FIGURE 2).

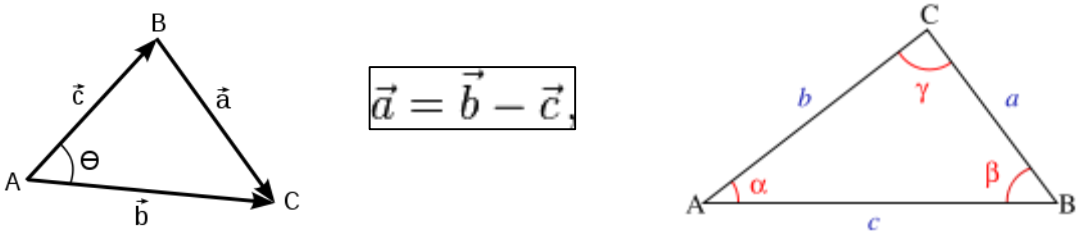

FIGURE 2 - left: vector triangle; middle: vector operations; right: the angles α (or A), β (or B), and γ (or C) are respectively opposite to the sides a, b, and c (source: http://en.wikipedia.org/wiki/Law_of_cosines)

This means that the corrected speed is calculated by:

$$\text{Corrected\_speed} = \sqrt{(\text{speed\_turt}^2 + \text{speed\_curr}^2 - (2 \times \text{speed\_turt} \times \text{speed\_curr} \times \cos(\text{final\_dir}))}$$

Where,

- speed_turt – velocity of the turtle at that location
- speed_curr – velocity of the current at that location
- final_dir – resultant vector between directions of the turtle and the current at that location

For the locations where there was no available data regarding the currents direction and magnitude, the speed was not corrected (meaning that the speed for that location was only calculated with distances/times). For the first location in each track, speed was considered “0”,

since that was the releasing location. Corrected speeds were then checked for values above 5 Km/h Hays et al. (2001), to assure that non-realistic velocities would not be included. Speed correction was performed in R (R Development Core Team 2011) (using packages: matlab (Roebuck 2011), circular (Agostinelli and Lund 2011) and argosfilter (Freitas 2012).

2.2.2.1 - Angles in relation to currents:

After determined the corrected speed, the obtained information about turtles and currents directions was also used to create plots containing the resultant angles between the bearing of the turtles in relation to the current at each location, to investigate if the animals tend to travel with or against the currents. For that purpose, classes were created for 3 angles (0^0, 90^0 and 180^0) and each location was assigned to a given class according to the following intervals resulting angle obtained:

- Class 0^0: [0^0; 44^0] and [316^0; 360^0]
- Class 90^0: [45^0; 135^0] and [226^0; 315^0]
- Class 180^0: [136^0; 225^0]

2.2.3 - Straightness Index (SI):

Straightness Index (SI) (Batschelet 1981) is the ratio of the beeline distance between the start and the end of a trajectory to total distance travelled (Postlethwaite et al. 2013). A higher sinuosity is associated with more turning angles, meaning that the animal is most likely to be foraging. If, by the contrary, the path is closer to a straight line, it means that the animal is most likely passing through (therefore, not foraging).

For each track, SI was calculated for a weekly (7 days) step-length, to make sure a sufficient number of locations were contained in that time length and that the sinuosity of the segment would be perceptible. Another reason for the 7 days step length choice is the usually weekly availability of the environmental data to be extracted later. SI was calculated by dividing the distance (km) of the weekly segment in a straight line by the distance travelled by the animal in that segment, using spherical trigonometry (Freitas 2013) (see details on formulae in Zwillinger (2003)). The values range from “0” (higher sinuosity will reflect values closer to “0”) and “1” (a straight line will have a value of “1”, which means that values closer to “1” will correspond to less sinuous segments). To all locations in each segment the same SI value is assigned. SI was performed in R (R Development Core Team 2011) (using packages: zoo (Zeileis and Grothendieck 2005) matlab (Roebuck 2011), circular (Agostinelli and Lund 2011) and argosfilter (Freitas 2012).

2.2.4 – Determining ARS for each method:

For each one of the previously described methods, ARS was determined, using R software (R Development Core Team, 2011), packages matlab (Roebuck 2011), circular (Agostinelli and Lund 2011), argosfilter (Freitas 2012) and zoo (Zeileis and Grothendieck 2005). The thresholds for considering ARS locations were, for FPT, values above the 3rd quartile (higher values of FPT) and for corrected speeds and Straightness Index, values below the 1st quartile (the lowest values for speed and straightness index). For each location, the resulting ARS was represented, by either "0" (corresponding to "not foraging" location) or "1" (corresponding to "foraging" location). For each track, the first position was considered ARS=0, whatever the output was, because it corresponded to the release position. ARS was determined separately for each method because the first attempt was to calculate ARS with all three parameters combined, but this was shown to be extremely restrictive, resulting in only a few ARS locations, which would be unrealistic, as turtles spend a great portion of their time foraging (TEWG 2009), and this would become more of a problem when environmental variables were to be analysed in relation to ARS regions. On the other hand, although each method by itself could be independently used to infer foraging areas, the purpose was to cross methods and restraint to some extent the final ARS regions. It was observed, by plotting ARS in ArcMap™ (ESRI 2011), that, by itself, each method would either classify almost the whole track (which happened with ARS determined by using FPT), or different regions of the path (which occurred with speed and SI ARS tracks). For that reason, methods were combined 2 by 2, which ultimately also enabled obtaining a scale for ARS and highlighting the regions where all three methods resulted in ARS locations. Procedures concerning methods' combination are explained in the subsequent paragraphs.

2.3 – Combining ARS determined by the different methods:

2.3.1 - Operations with ARS previously determined for each method:

After determining ARS for all the 10 tracks for each method, the resulting tracks were added in ArcMap™ (ESRI 2011). Using the "point to raster" tool, rasters were created for ARS (for each track), using the "maximum" cell assignment type (the maximum value of the attributes of the points within the cell, which means that the resulting cell will either have a value of "1", if one or more points within that cell have ARS=1, or "0", if none of the points within that cell have ARS=1). Spatial resolution chosen for these rasters was 0.25, based in ARGOS

maximum error of 10 km (see Hays et al. (2001)) and also to be coherent with the available spatial resolution of the environmental remote sensed data that will be later extracted.

Using ArcMap raster calculator (in spatial analyst tools), the previous created rasters were multiplied 2 by 2, for each track, as follows:

- $ARS_{(fpt \times si)} = ARS_{(fpt)} \times ARS_{(si)}$
- $ARS_{(fpt \times speed)} = ARS_{(fpt)} \times ARS_{(speed)}$
- $ARS_{(si \times speed)} = ARS_{(si)} \times ARS_{(speed)}$

where $ARS_{(fpt)}$, $ARS_{(si)}$ and $ARS_{(speed)}$ are the ARS rasters created for each parameter (FPT, SI, speed). This means that the resulting rasters would only have, for each pixel, a value of "1" if the two multiplied rasters had the value "1" for that cell.
Then, using the same tool, a sum of the resulting rasters was made for each track:

$$ARS_{(final)} = ARS_{(fpt \times si)} + ARS_{(fpt \times speed)} + ARS_{(si \times speed)},$$

where ARS (final) rasters would either have, for each pixel, a value of:

- "0" - if none of the previous combinations had "1" for that cell (meaning that none or only one of the three parameters had value "1" in the cell)
- "1" – if one of the previous combinations had "1" for that cell (meaning that two of the three parameters had value "1" in the cell)
- "3" - if all of the previous combinations had "1" for that cell (meaning that the three parameters had value "1" in the cell)

The value "2" never shows up because if two of three combinations have value "1" for a certain pixel, this means that the third combination will also necessarily be "1" (e.g.: if A x B = 1 and B x C = 1, it means that A x C will also be 1, because in a universe of "0" and "1" values, the only possible way to have a value of "1" in two combinations is to have A = 1, B = 1 and C = 1).

The final rasters were converted to ESRI shapefiles, with the "raster to point" tool, and merged into one. For a better visualization, points with ARS = 1 and ARS = 3 were highlighted with circles with different sizes and colours.

2.3.2 - Separating tracks by seasons:

To visually understand the possible interaction between seasons and the latitudes occupied by the turtles, ARS resulting shapefiles were grouped by tagging seasons (which means that 5 shapefiles were grouped as spring-tagged and the other 5 shapefiles were grouped as autumn-tagged, according to the seasons that the turtles were tagged).

To refine the relationship between seasons and animals' foraging environmental choices, each one of the 30 tracks that resulted from ARS calculation (10 tracks for each parameter) was separated in its seasons' segments and the above procedures previously performed for each track (combination of ARS determined by the different methods) was applied to each segment, by season and year (meaning that each season portion of an ARS track determined by one method was combined with the exact same season portions determined by the other two methods). Seasons were defined as follows (TABLE 6):

TABLE 6 - Months that correspond to each season

	Mar-May	Jun-Aug	Sep-Nov	Dec-Feb
spring				
summer				
autumn				
winter				

2.4 – Oceanographic variables:

2.4.1 – Extracting environmental variables:

To extract all the variables of interest, Marine Geospatial Ecology Tools (MGET) (Roberts et al. 2010) was used, and all the procedures were performed in ArcMap™ (ESRI 2011). The following variables were extracted: bathymetry (m), sea surface temperature (SST) (^{0}C), sea surface height (SSH) (cm), sea surface high anomalies (SSHA) (cm), chlorophyll *a* (Chl*a*) (mg/m^3). The tracks were added in ArcMap™ (ESRI 2011) and the environmental variables were interpolated at points, for each track. Interpolation method chosen was "nearest" (interpolated value for each point is the value of the cell that contains the point). Besides interpolation at points, 8-day, monthly, 3 months, annual and cumulative gridded maps were also extracted for each variable for better visualization in relation to the previously determined ARS. Cumulative maps were extracted by defining the beginning and the end dates of the

extraction as the tracking time (from 01-04-1998 to 16-08-1999). Details concerning the environmental variables and their providers are described below:

2.4.1.1 - Bathymetry:

General Bathymetric Chart of the Oceans (GEBCO) 500 gridded bathymetry data was extracted, available from the British Oceanographic Data Centre (http://www.bodc.ac.uk). Values for bathymetry were also extracted for each location of the turtles' tracks, using the "extract multivalues to points" tool, in ArcMap™ (ESRI 2011).

2.4.1.2 - Sea surface temperature (SST):

Global Blended Sea Surface Temperature was extracted from the Group for High-Resolution Sea Surface Temperature (GHRSST). This product is hosted by NASA JPL Physical Oceanography Distributed Active Archive Center (PO.DAAC) and is provided on a level 4 (L4) gap-free, 0.25 degree grid. Level 4 data are model output or results from analyses of lower level data (e.g., variables derived from multiple measurements). This product uses optimal interpolation (OI) using data from the 4 km Advanced Very High Resolution Radiometer (AVHRR) Pathfinder Version 5 time series (when available, otherwise operational NOAA AVHRR data are used) and in situ ship and buoy observations. The OI analysis is a daily average SST that is bias adjusted using a spatially smoothed 7-day in situ SST average. To fill in cloudy areas, data from multiple satellite and in-situ sensors are combined and regions without any data are filled in various interpolation and modelling techniques (http://podaac.jpl.nasa.gov/dataset/NCDC-L4LRblend-GLOB-AVHRR_OI).

2.4.1.3 - Sea surface height (SSH):

Global delayed-time (DT) updated (Upd) merged MADT (Maps of Absolute Dynamic Topography) SSH gridded product was extracted from AVISO (http://www.aviso.oceanobs.com/duacs/) with a weekly temporal resolution and spatial resolution of 1/4°x1/4° on a Cartesian grid. This is a product of gridded sea surface heights above geoid (shape of the sea surface assuming a complete absence of perturbing forces (tides, wind, currents, etc.) and is the sum of sea level anomaly (SLA) and mean dynamic topography (MDT), both being referenced over a 7 year-period, between 1993 and 1999.

According to AVISO, weekly images are not created by aggregating the daily products together (they are not produced taking mean of seven daily images, for example). They are,

instead, a sparse selection of the daily images: every seventh daily image exactly matches a weekly image, pixel for pixel (see AVISO: (http://www.aviso.oceanobs.com/duacs/) for more details).

2.4.1.4 - Sea surface height anomalies (SSHA):

Global delayed-time (DT) updated (Upd) merged MSLA (Maps of Sea Level Anomalies) SSH gridded product was extracted from AVISO (http://www.aviso.oceanobs.com/duacs/) with a weekly temporal resolution and spatial resolution of 1/4°x1/4° on a Cartesian grid. This product corresponds to the variations of the sea surface height with respect to a several-year mean or a mean sea surface and its variability (the standard deviation over time) is somewhere between 2-3 cm and 60 cm, depending on energy levels in different parts of the ocean. While the MADT data are the actual SSH or geostrophic currents, the MSLA data are anomalies, i.e. the differences from a multi-year mean of SSH or currents.

As for SSH, weekly images are not created by aggregating the daily products together (they are not produced taking mean of seven daily images, they are a sparse selection of the daily images: every seventh daily image exactly matches a weekly image, pixel for pixel (see AVISO: (http://www.aviso.oceanobs.com/duacs/) for more details).

2.4.1.5 - Chlorophyll *a* (Chl*a*):

Chl*a* Level 3 (these data are the derived geophysical variables binned/mapped to a uniform space/time grid scale) SMI (Standard Mapped Image) product was extracted from NASA Goddard Space Flight Center (GSFC) OceanColor Group (http://oceancolor.gsfc.nasa.gov/), using Sea-viewing Wide Field-of-view Sensor (SeaWiFS), with 8 day temporal resolution and 9 km spatial resolution.

For better visualization, a log-transformation was also applied to the extracted Chl*a* cumulative map, by using the raster calculator, available in spatial analyst tools, in ArcMap™ (ESRI 2011).

2.4.2 – General procedures:

For all the extracted variables and for each track, rasters were created with the “point to raster” tool, using the “mean” filter (each pixel corresponds to the mean of the points within that pixel), and with a 0.25 cell size. Points that had no available data for any of the environmental extracted variables were first removed to create the raster for that variable. Using Spatial

analyst tool (cell statistics), a global raster for each variable was then created, by assembling all rasters for that variable, and creating a single raster with the mean.

The same way that it was performed for ARS, environmental variables tracks were grouped by tagging seasons (for each variable). Each track was also split by season and rasters were created for each track segment. These rasters were then grouped by season and year and a global raster was created for each season and year, with the mean filter.

2.4.3 - Creating histograms for variables and ARS

Density histograms of ARS locations were created for each one of the extracted variables, using "density histogram to field" tool, available in MGET (Roberts et al. 2010), and this procedure was performed in ArcMap™ (ESRI 2011).

2.5 – Applying a Generalised Additive Model (GAM):

The idea of applying a model to the data is to try to represent a process using a range of variables that may be influencing that process. In this case, the process is the foraging behaviour of the tagged turtles, here represented by ARS, and the variables that may be influencing this behaviour are the environmental parameters extracted (bathymetry, SST, SSH, SSHA, Chl*a*).

Generalised additive models (GAMs) (Hastie and Tibshirani, 1990) are an extension of generalised linear models (GLMs) that allow the incorporation of nonlinear predictor effects using smooth functions (smoothers) of the predictor variables (Venables and Dichmont 2004). A smoother is a tool for summarizing the trend of a dependent variable Y as a function of one or more independent variables. These tools are very useful in statistical analysis, because they allow to first, visualize the trend from the plots and then estimate the dependence of the mean of Y on the predictors (Venables and Dichmont 2004). Due to their non-parametric nature, smooth functions don't assume a rigid form for the dependence of Y on X1, …, Xn, and instead, allow an "approximation" with sum of functions (these functions have separated input variables), not just with one unknown function only (Venables and Dichmont 2004). GAMs' strength lies in their ability to deal with highly nonlinear and non-monotonic relationships between the response and the set of explanatory variables, which makes them ideal for expressing underlying relationships in ecological systems (Mugo et al. 2010). Moreover, they can be used to identify optimal conditions for a given species using environmental variables in order to predict the likelihood that a given species would inhabit a particular environment (Drexler and Ainsworth 2013).

2.5.1 Preparing the tracks to fit the GAM

To apply a GAM to the data, the first step was to create tables containing ARS values determined by each method as well as the values of the extracted environmental variables, for each track. Locations that had no available data for any of the environmental variables extracted were removed, to make sure that all the variables would be considered when fitting a GAM. Another reason to exclude segments containing missing values of the explanatory variables is that mgcv package does not have a function to account for missing values of the covariates (Dalla Rosa et al. 2012).

Tracks were all assembled and, for each location, ARS determined by each method (FPT, corrected speeds and SI) were combined in EXCEL (Microsoft® Office 2010), by multiplying the ARS cells 2 by 2, for each track, the same way ARS rasters were combined in ArcMap™ (ESRI 2011):

- $ARS_{(fpt \times si)} = ARS_{(fpt)} \times ARS_{(si)}$
- $ARS_{(fpt \times speed)} = ARS_{(fpt)} \times ARS_{(speed)}$
- $ARS_{(si \times speed)} = ARS_{(si)} \times ARS_{(speed)}$

where $ARS_{(fpt)}$, $ARS_{(si)}$ and $ARS_{(speed)}$ are the ARS tables created for each parameter. This means that the resulting cell will only have a value of "1" if the two multiplied values were "1". Then, a sum of the resulting cells was made for each track:

$$ARS_{(final)} = ARS_{(fpt \times si)} + ARS_{(fpt \times speed)} + ARS_{(si \times speed)},$$

and ARS (final) cells will either have a value of:

- "0" - if none of the previous combinations had "1" for that cell (meaning that none or only one of the three parameters had value "1" in the cell)
- "1" – if one of the previous combinations had "1" for that cell (meaning that two of the three parameters had value "1" in the cell)
- "3" - if all of the previous combinations had "1" for that cell (meaning that the three parameters had value "1" in the cell)

For the same reason of rasters combination results, the value "2" never appears. To apply a GAM, values of "3" were transformed in "1", meaning that ARS locations would be considered whenever two of the three methods had value "1". This process was made to be consistent with the previous ARS rasters combination performed in ArcMap™ (ESRI 2011).

A final table containing the response variable (ARS) and the predictors (environmental variables) was produced and the predictors' values were trimmed, by defining a minimum and maximum for each predictor, according to the values where only a few locations would fall in, to enable a better interpretation of the resulting plots (see TABLE 7).

TABLE 7 - Environmental variables minimum and maximum trimming

Variable	Min	Max	Min (trimmed)	Max (trimmed)
SST (^{0}C)	11.92	24.92	15	24.92
SSH (cm)	-32.61	72.96	0	50
|SSHA| (cm)	0	43.92	0	20
Log-transformed [Chl*a*]	-3.62	2.74	-3	1
Bathymetry (m)	-5620	-2	-5000	-2

2.5.2 Variables correlation:

After adding the final table to ArcMap™ (ESRI 2011), possible correlation between variables were investigated using the tool "Scatterplot Matrix for Table", available in MGET (Roberts et al. 2010). This tool uses R pairs function and produces plots for the designated variables and displays values and scatterplots of the correlation between each two variables (and also line fitted using the LOWESS smoother). Pearson's correlation coefficient (r) was used to assess which variables may be included in the same model, without the interference of being correlated. Although this method is usually referred to as requiring normal distributions of the variables, which may not be the case for all variables, it has been found to have significant advantages for continuous non-normal data which does not have obvious outliers (Chok 2008). Thus, the shape of the distribution should not be a sole reason for not using the Pearson product moment correlation coefficient. Values range from "-1" (perfectly negatively correlated variables) to "1" (perfectly positively correlated variables). A value of "0" denotes no linear correlation. According to Evans (1996), the strength of the correlation for the absolute value of "r" is defined as follows:

- 0 - 0.19: "very weak"
- 0.20 – 0.39: "weak"
- 0.40 – 0.59: "moderate"
- 0.60 – 0.79: "strong"
- 0.80 – 1.0: "very strong

Based on this scale and in previous works (Gorman et al. 2013), the threshold for considering high correlation was 0.6 (“strong correlation”), which means that paired-variables with a coefficient above 0.6 were included in separate competing models.

2.5.3 Fit GAM:

A GAM was fitted to the data, using Marine Geospatial Ecology Tools (MGET) (Roberts et al. 2010) statistics “Fit GAM”. MGET uses R (R Development Core Team 2011) packages to fit the model. The selected package to fit the GAM was mgvc (Mixed GAM Computation Vehicle) (Wood 2011) as this package is under active development and maintenance and provides more features than the gam package. Particular features of this package are facilities for automatic smoothness selection (Wood 2011), and the provision of a variety of smoothers of more than one variable.

A Bayesian approach to smooth modelling is used to derive standard errors on predictions, and hence credible intervals (Marra and Wood 2011). To fit the model, data was first randomly split into training and test data, using MGET (Roberts et al. 2010). Therefore, 2/3 of the data were randomly selected as training data and 1/3 were randomly selected as test data, for model validation. The model was first fitted to the previously random selected 2/3 of the data, using the formula:

ARS ~ s(SST) + s(SSH) + s(|SSHA|) + s(log-transformed [Chl*a*]) + s(bathymetry)

where ARS is the response variable and the predictors are the environmental variables. “s” is a thin plate regression splines smoothing function. Also, for the model, absolute values of variable SSHA (sea surface height anomalies) were used, and variable Chl*a* values were log-transformed. GAM was fitted using binomial family and default automatic smoothness selection (logit function, smoothing parameter estimation method GCV.cp, optimizer outer and alternative optimizer newton). Smoothing parameters are estimated by minimizing the GCV score. A "double penalty approach" for smoothing parameter estimation was applied (Marra and Wood (2011). This is an alternative mechanism for allowing mgcv to shrink terms completely to zero, rather than specifying shrinkage smoothers on individual model terms. A summary table containing the significance of the smooth terms is produced, as well as a plot for each smooth term (for more details, see Wood 2011).

2.5.4 Model Validation:

Model validation was performed with the remaining 1/3 of the data ("test data"), using the "predict GAM from table" tool in MGET (Roberts et al. 2010). This tool predicts the response variable for each row of the table and outputs statistics that summarize how well the model's predictions match the observed values of the response variable (Roberts et al. 2010). This is achieved by using receiver operating characteristic (ROC) curve, which plots true positive rate (sensitivity) against false positive rate (specificity). For this analysis, a cutoff was automatically calculated from the training data, by selecting the value that maximizes the value of the Youden Index (Youden, 1950) (Perkins and Schisterman 2005). This Index is the most commonly used criterion because it reflects the intention of maximizing the correct classification rate (Kumar et al. 2011). Probabilities greater than or equal to the cutoff are classified as 1 and probabilities less than the cutoff are classified as 0. The area under the ROC curve (AUC) is a widespread measure of the overall diagnostic performance and its scale ranges from 0 to 1, where an AUC score of 0.5 means that the model has no better than random performance, while higher scores indicate improving accuracy (McClellan et al. 2014). For wide distribution species, like marine turtles, AUC values are typically lower (Phillips et al. 2009).

2.5.5 Model selection:

Model selection was performed between several models containing separately the correlated variables and was assessed through comparisons of the minimized Un-Biased Risk Estimator score (Zuur et al. 2010) and higher percentage deviance explained (Dalla Rosa et al. 2012, Gorman et al. 2013). AUC higher values obtained were also used to complement selection of best model fit. The selected formula was then applied to the entire dataset (Wood 2011).

3 - RESULTS

3.1 – General results:

The turtles were tracked for 56 days (ID12574) to 342 days (ID12547), with distances travelled ranging from 857 km (ID12574) to 8324 km (ID12545) (see TABLE 8). Mean velocity of all the turtles was 21.26 cm/s, and it ranged from 16.25 cm/s (ID 12570) to 38.88 cm/s (ID 12545). The turtle with the higher mean speed was also the one travelling the greater distance (ID 12545).

TABLE 8 - Summary information of the 10 tracks.

ID	Initial Date	Final Date	Tracked days	Distance (km)	Mean speed (cm/s)
12007	10-09-1998	16-06-1999	279	4290	17.50
12538	27-05-1998	01-11-1998	158	2883	20.74
12544	01-04-1998	30-12-1998	273	4785	19.43
12545	18-05-1998	19-02-1999	277	8324	38.88
12546	18-05-1998	03-09-1998	108	2436	26.04
12547	27-05-1998	04-05-1999	342	5482	19.48
12570	10-09-1998	18-07-1999	311	4453	16.25
12571	10-09-1998	16-08-1999	340	5407	19.52
12573	10-09-1998	10-01-1999	123	1811	17.82
12574	10-09-1998	05-11-1998	56	857	16.93

As it was previously mentioned, 5 turtles were tagged in spring (April and May) and 5 turtles were tagged in autumn (September). All the spring-tagged turtles, except one (ID 12547) headed NW from the release point and all the autumn-tagged turtles, except one (ID 12573) travelled SE (FIGURE 3). A larger image of the general map, and also both spring-tagged and autumn-tagged maps, are available in APPENDIX I (FIGURES 1 to 4).

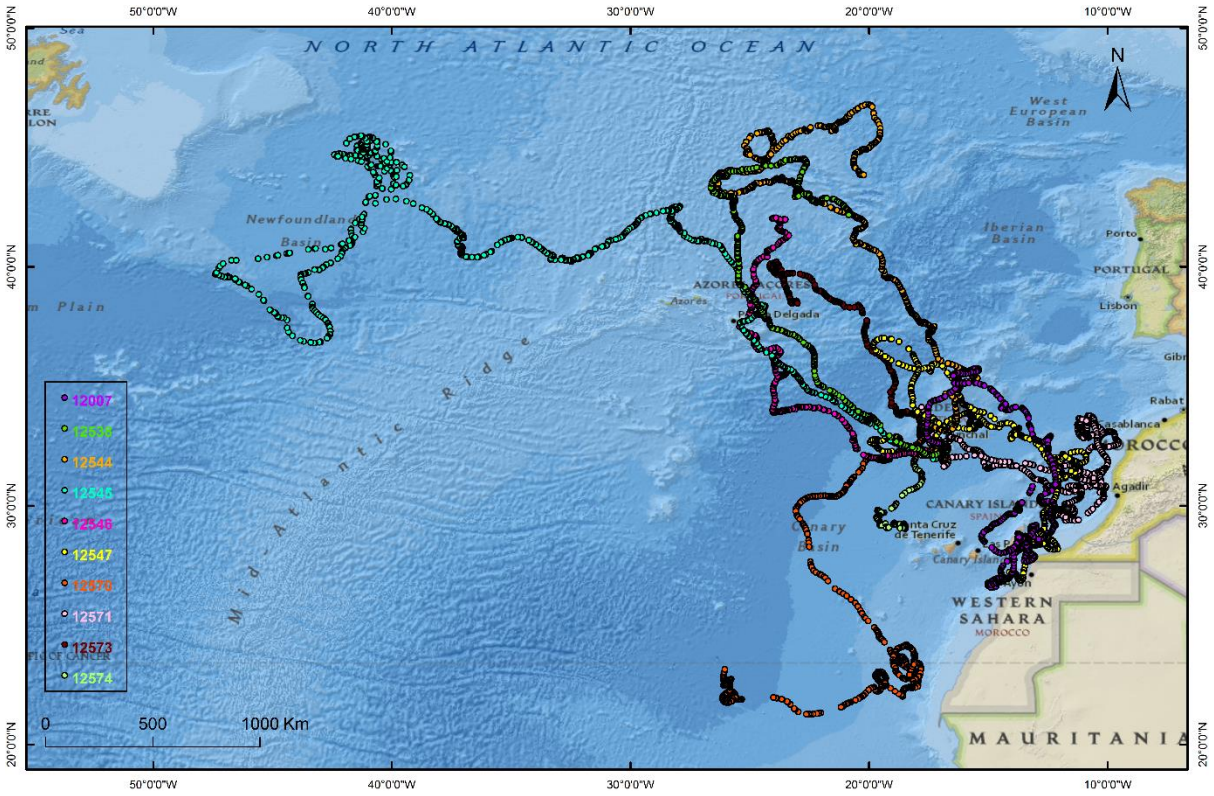

FIGURE 3 - General visualization of the turtles' tracks (original positions corrected with SSM-KF) plotted over National Geographic Basemap (available in ArcMap™ (ESRI 2011))

Autumn-tagged turtle ID 12573 travelled in the same direction of the spring-tagged turtles (NW), and spring-tagged turtle ID 12547 performed a slightly different initial path than the others, as this animal remained for about 4 months around Madeira, then travelled north, spending almost the entire fall at slightly higher latitudes, and then headed SE (the same direction of autumn-tagged turtles), during winter, where it spent the remaining months, until transmitter stopped sending messages (May 1999). The reasons why the tags stopped transmitting is unknown, but it could have been caused by failure or detachment of the transmitter, depletion of battery power, or by the death of the turtle (Polovina et al. 2004).

Autumn-tagged turtles IDs 12007 and 12571 and spring-tagged turtle ID 12547 all headed towards the same region, off the coast of Morocco, where they remained for winter 1998 and spring 1999. From these 3 turtles, one of them, ID 12571, after spending about 8 months (November-June) in that region, started to head NW and quickly reached the waters of Madeira again, and was continuing to travel NW when tag stopped transmitting (August 1999). Autumn-tagged turtle ID 12570 also remained for winter 1998 and spring 1999 in a region off the coast of Africa, but at lower latitudes (Western Sahara latitude).

All spring-tagged turtles, except ID 12547, headed to a region located NE from Azores, within mid latitudes, in relation to their limits, where most of them remained for summer and autumn, until the tags stopped transmitting. 3 of the 5 spring-tagged turtles passed through

Azores when heading to that region. There is no clear information about the wintering directions of these 3 turtles, as track from ID 12544 is the longest and still, it ends in December 1998. Autumn-tagged turtle ID 12573 also headed to close regions of these spring-tagged turtles, where the animal remained during December 1998, and it appeared to be heading south when transmissions stopped.

Another interesting feature was visible in spring-tagged turtle ID 12545 (the one performing the longest distance) (image available in APPENDIX I, FIGURE 5). This turtle travelled NW like the other spring-tagged turtles, but in September, the animal headed east for the winter, and reached the Flemish Cap at the end of December, remaining in that region until transmissions ended (February 1999).

As it is possible to observe in FIGURE 4, which relates occupied latitudes with seasons, there is not a unique pattern in the latitudes occupied by the turtles during each season, as some turtles tend to occupy higher latitudes while others remain in lower latitudes. There is, however, at least for some data, a trend for heading to higher latitudes in the summer and for occupying lower latitudes in the winter. Occupied latitudes ranged from 21.26^{0}N (lower limit) to 46.79^{0}N (higher limit).

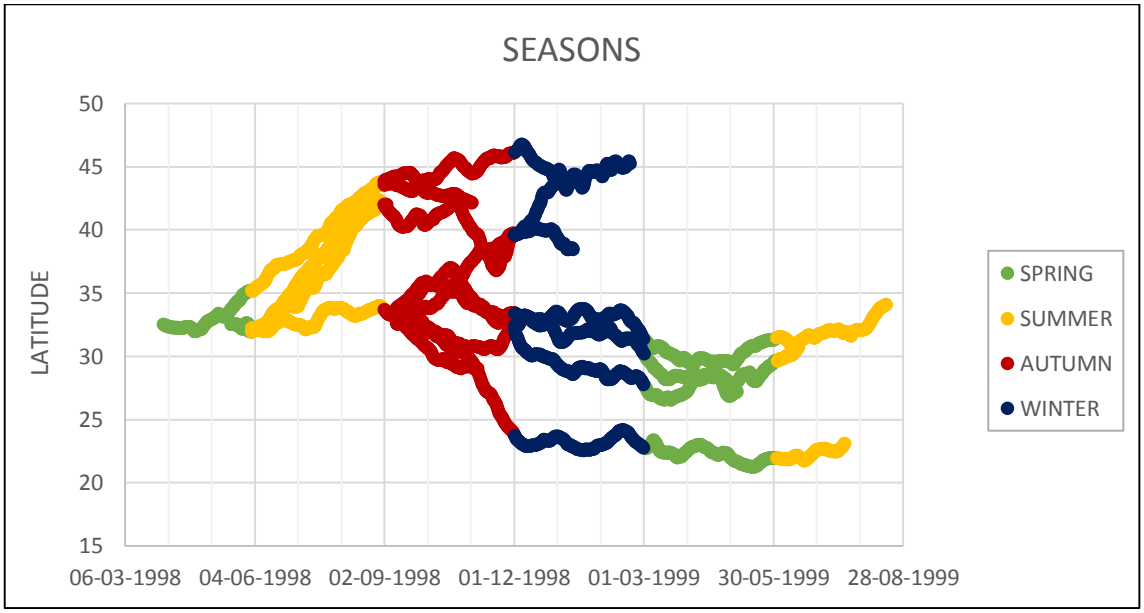

FIGURE 4 - Graph showing latitude variability with seasons

.

By analysing the turtles' paths segmented by each season, it is possible to see that, in general, the animals tended to occupy their higher and lower latitude limits in winter and spring, but remaining within a narrow region during these seasons, while in summer and autumn they travelled longer distances, occupying a larger area (see APPENDIX I, FIGURE 6).

Output plots of comparison of the turtles' bearings in relation to current's direction for each location indicate that for most of the locations, the turtles were not swimming against nor in favour to the currents, as all turtles presented a clear higher density of 90^0 angles to current (see APPENDIX II, FIGURE 31). However, 9 of the 10 turtles had a higher density of 0^0 ("with the current") angles than 180^0 ("against the current"), and only turtle ID 12571 had a higher density of 180^0 angles.

3.2 – Area-restricted search (ARS):

From a total of 3202 locations that were used to apply the GAM (only locations which had values for the environmental variables extracted were used to fit the model), 653 locations (20.39%) correspond to ARS=1 (foraging locations) (TABLE 9). These results include all 10 tracks. Analysis of individual tracks show that spring-tagged ID 12545 was the turtle with the highest % of foraging locations (25.36% ARS locations) and the one with the lowest % was autumn-tagged ID 12007 (16.38% ARS locations).

TABLE 9 - Total number of locations for all tracks and ARS=1 locations; these locations are the total number that had values for extracted environmental parameters.

ID	Locations		
	ARS	**Total**	**% ARS**
12007	67	409	16.38
12538	57	234	24.36
12544	85	352	24.15
12545	71	280	25.36
12546	36	183	19.67
12547	96	499	19.24
12570	83	451	18.40
12571	94	540	17.41
12573	38	151	25.17
12574	26	103	25.24
TOTAL	653	3202	20.39

By plotting the resulting ARS (FIGURE 5) (larger image available in APPENDIX I, FIGURE 7), it is possible to observe that ARS locations exist in different regions along the turtles' paths. However, there are some specific regions where the amount of ARS locations

is higher. One of those regions is the off-coast of Morocco, which was previously referred to be a common area where some of the turtles remained for the wintering months. This region was also the area where more “three parameters ARS” exist (ARS determined by all methods occurred for that location), highlighted by red circles. Other regions where ARS is quite notable are located NE of Madeira and Azores. Some specific ARS regions are unique for some individuals. Turtle ID 12570 exhibits a high amount of ARS locations in the waters off the coast of Africa, but at lower latitudes than the other turtles that occupied this region, and turtle ID 12545 exhibits ARS at the Flemish Cap region. These two turtles were the only ones that headed for these two specific regions.

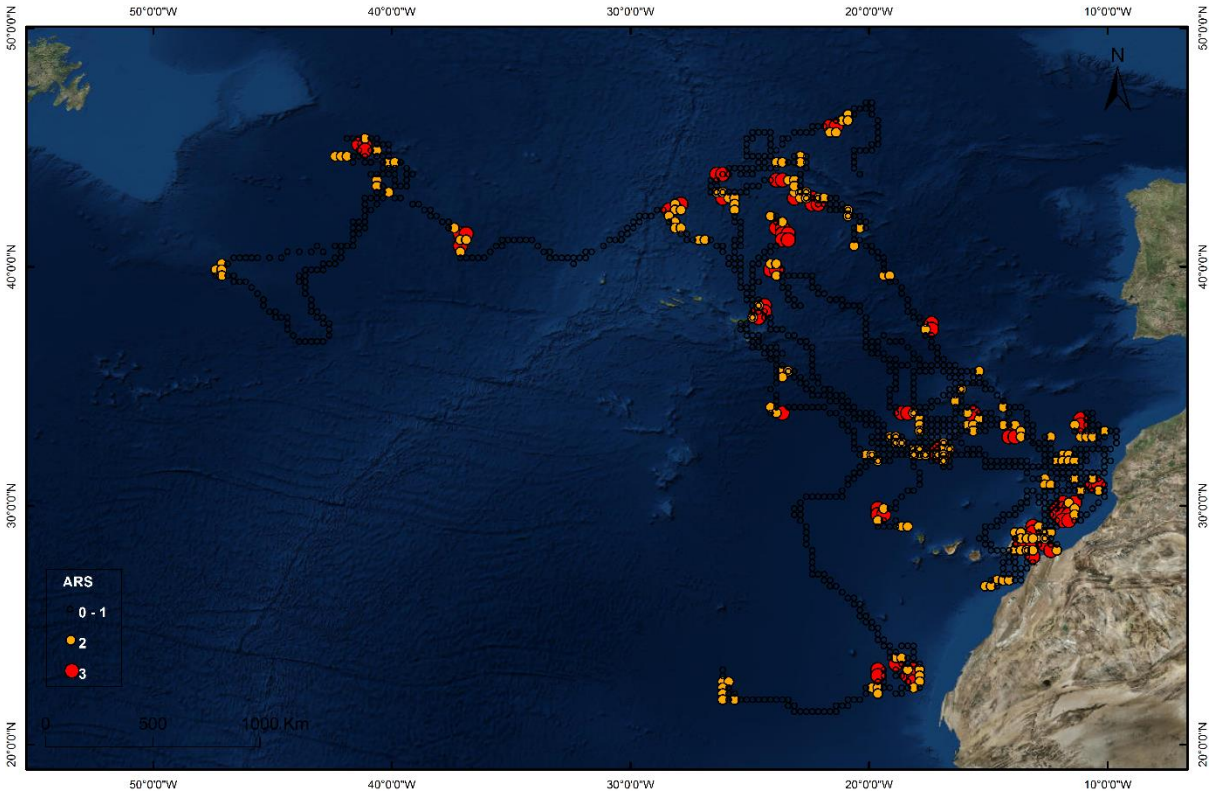

FIGURE 5 - ARS results plotted over Google Earth Basemap (available in ArcMap™ (ESRI 2011))

3.2.1 - Area-restricted search (ARS) and seasons:

By analysing ARS occurring within each season, it is possible to observe that almost all of the spring-ARS occurred near the African coast. In fact, ARS for spring of 1999 occurred exclusively in that region. The other region where ARS occurred in spring was near the release point, for spring-tagged turtles, shortly after the release date. In summer, ARS occurred mostly between Madeira and a region located NE of Azores. This is true for all ARS occurring during the year of 1998, but in 1999, ARS occurred at lower latitudes (near the African coast, as it

was observed in spring, for turtle ID 12571, and at Western Sahara latitude, for turtle ID 12570). ARS occurring during autumn and winter only exist for the year of 1998, as the last tracked day was August 16th 1999. For these seasons, there is not a unique pattern for ARS occurrence, as it is possible to visualize scattered ARS locations within many regions. For turtles that travelled north, ARS occurred mostly at NE from Azores (ID 12545 was the only exception, with ARS occurring during this animal's path heading east). For the turtles that headed south, ARS during autumn and winter occurred between the release point and the African coast, with a few ARS occurring near the Eastern Canary Islands. Maps concerning ARS by season are available in APPENDIX I, FIGURES 9 to 12.

3.2.2 – Area-restricted search (ARS) and oceanographic variables:

General results concerning the oceanographic variables mean values for ARS=0 and ARS=1 locations and for all turtles are presented in APPENDIX III, TABLE 1.

3.2.2.1 - Bathymetry:

The tracked turtles travelled within bathymetry ranges of -5620 m and -2 m, with a mean value for bathymetry along the positions for all turtles of -3238 m. Considering only ARS=1 locations, the mean bathymetry value correspond to a slightly lower bathymetry (-2980 m) (see APPENDIX III, TABLE 1).

By plotting ARS over a bathymetry map, it is possible to visualize that almost every regions containing more ARS locations also are low bathymetry regions (FIGURE 6) (larger image available in APPENDIX I, FIGURE 13). On the other hand, there are some large areas of low bathymetry regions relatively close to the paths of some of the turtles that were almost completely neglected by them, as it is possible to observe in the waters surrounding Azores. This area includes a portion of the Mid-Atlantic Ridge and consists in a low bathymetry large area and, although 4 of the 10 turtles (IDs 12538, 12545, 12546 and 12573) travelled nearby, they only used the right limit of this large region. Nevertheless, for every mentioned turtle, ARS occurred in those regions. A detail map concerning low bathymetry regions is available in APPENDIX I, FIGURE 14.

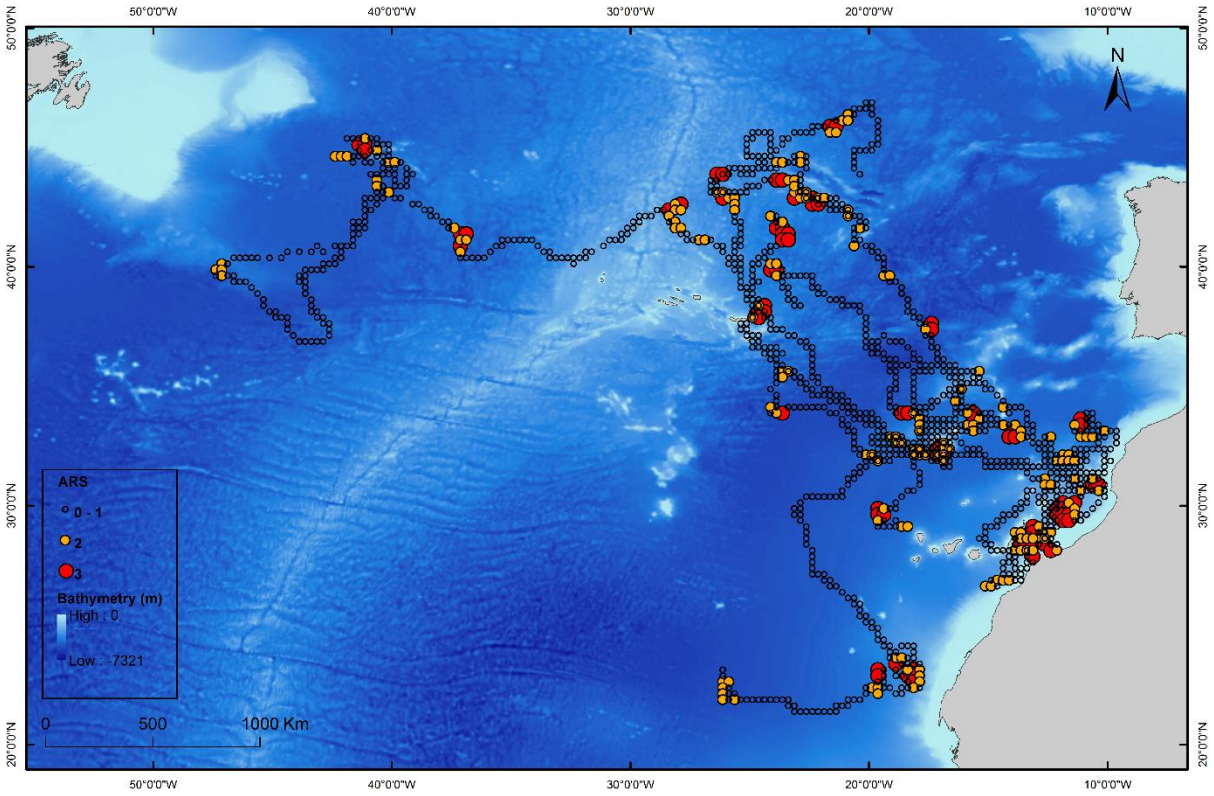

FIGURE 6 - ARS results plotted over GEBCO bathymetry map (larger image available in APPENDIX I, FIGURE 13)

3.2.2.2 – Sea surface temperature (SST):

The turtles travelled between sea surface temperature ranges of 11.92 ^{0}C and 24.92 ^{0}C, with a mean temperature of 20.36^{0}C. It is possible to observe that, for ARS=1 locations, the mean SST value is slightly lower (19.73 ^{0}C) (see APPENDIX III, TABLE 1).

A visual analysis of the tracks plotted over a cumulative mean SST gridded map (FIGURE 7) shows that these animals tend to occupy the mid temperatures within their range, by not travelling within neither too high or too low temperatures.

Although it is not evident for all ARS locations, it is possible to visualize that for many ARS regions, temperature tends to be lower or in between the boundaries of lower and higher temperatures, as it is showed in the regions near the African coast and in the Flemish Cap. However, there are some regions where this is not that clear, which is the case of ARS locations occurring in the waters near Madeira, with mid-ranges temperatures.

By plotting spring-tagged and autumn-tagged turtles independently over 3 months SST gridded maps (maps available in APPENDIX I, FIGURES 16 to 19), it is possible to observe that the turtles followed temperature seasonality variations as, in general, spring-tagged turtles headed to higher latitudes where temperature were not so high, and autumn-tagged turtles headed to lower latitudes, where temperatures were not so low, for the winter months.

However, both lower and higher latitude limits achieved by the turtles correspond to mostly winter months, and it is possible to observe (TABLE 10) that mean SST was lower during winter and higher in the summer.

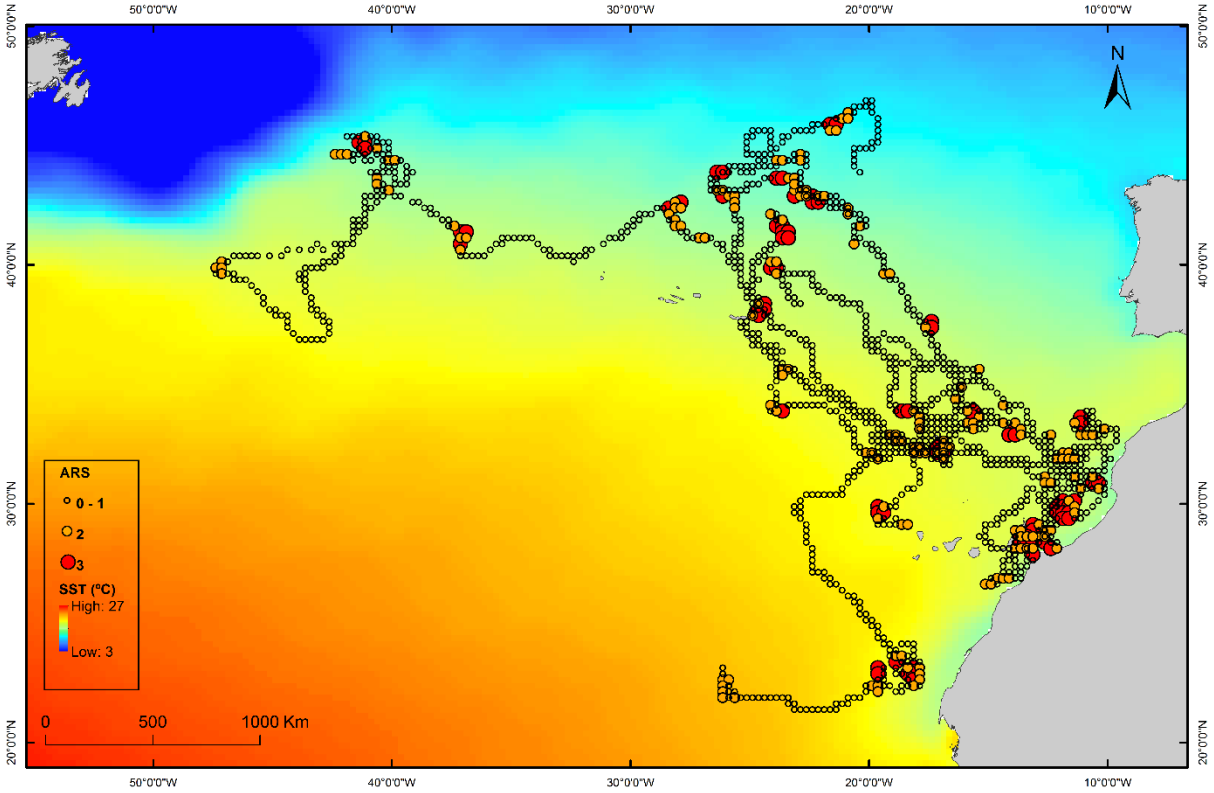

FIGURE 7 - ARS results plotted over a cumulative SST gridded map (larger image available in APPENDIX I, FIGURE 15)

TABLE 10 - SST (ºC) ranges during seasons for all the 10 turtles.

		spring	summer	autumn	winter
SST (^{0}C)	Min	15.70	17.55	15.94	12.50
	Max	23.22	24.80	24.57	21.38

3.2.2.3 – Sea surface height (SSH):

The turtles travelled within a maximum SSH of 72.96 cm and a minimum SSH of -32.61 cm, with a mean SSH value of 20 cm. For ARS=1 locations, the mean SSH value is slightly lower (18.10 cm) (see APPENDIX III, TABLE 1).

Although there are not many obvious visual aspects relating most of the tracks with the use of extreme SSH values (FIGURE 8), by plotting them over a cumulative SSH gridded map, there is one turtle that shows to have used the lower and the higher SSH values. This turtle, ID 12545, spent the last tracked few months foraging within the lower and the higher SSH limits obtained for all tracks (detail map available in APPENDIX I, FIGURE 21) along eddies occurring within the boundaries between Gulf and Labrador currents. For the other turtles,

although they were not travelling through such high SSH ranges as turtle ID 12545, ARS regions occurred mostly in their higher and lower limits of SSH values.

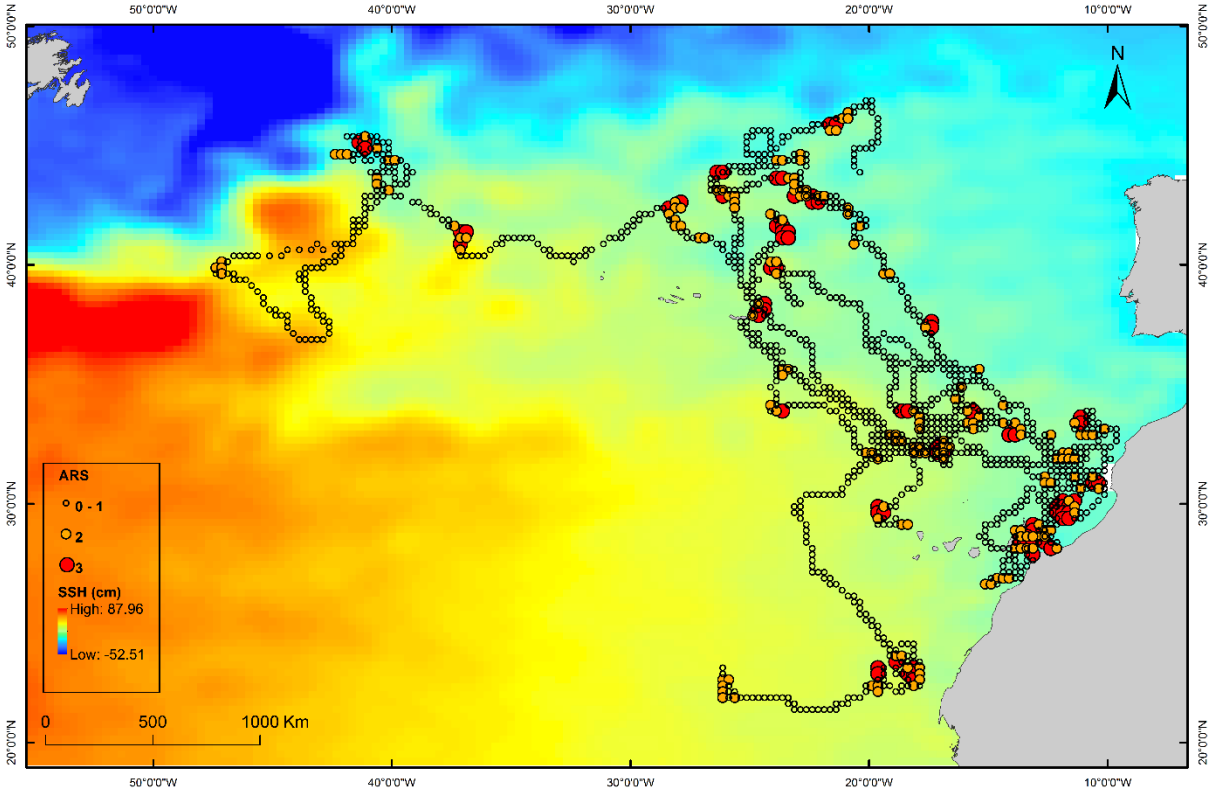

FIGURE 8 - ARS results plotted over a cumulative SSH gridded map (larger image available in APPENDIX I, FIGURE 20).

3.2.2.4 – Sea surface height anomalies (SSHA):

The turtles travelled within ranges of SSHA values of -43.92 cm and 42.11 cm, with an average SSHA value of 2.09 cm, throughout all the tracks. Considering only ARS=1 locations, the mean SSHA value is lower (0.90 cm) (see APENDIX III, TABLE 1 for more details). In terms of absolute SSHA values, mean values are very close to each other, with the mean ARS=1 locations value being only slightly higher (5.72 cm) than the same value for all the locations (5.40 cm).

By plotting ARS over a weekly cumulative mean SSHA gridded map (from the beginning until the end of the tracking time) (FIGURE 9), it is possible to see that most of the higher concentration of more pronounced eddies occurred NW from the release point, where only one of the turtles (ID 12545) headed to. The occurrence of ARS in areas with the higher and lower values of sea level anomalies is evident for some turtles. This feature is particularly visible for the final 3 months of tracking for turtle ID 12545, where the animal spent the month of December foraging in a region with high positive values of sea level anomalies (warm-core

eddy), and then travelled to another region with high negative values of SSHA (cold-core eddy), for the last two months of tracking (January and February). For other turtles (IDs 12538, 12544, 12546 and 12573), ARS also matches regions where the presence of warm-core eddies is high, mostly NE from Azores. This visual relation between turtles' ARS and SSHA was more obvious for the turtles travelling north, which includes most of the spring-tagged turtles (except turtle ID 12547) and autumn-tagged turtle ID 12573. For the remaining turtles, which foraged mostly within the African off-coast region, there is apparently no clear relation between ARS and sea surface height anomalies. In general, the animals appear to mostly use eddies' edges, particularly for warm-core eddies (high values of SSHA), as it is visible in detail maps for some of the turtles travelling NW (APPENDIX I, FIGURES 24 to 26). However, by plotting ARS over the last month of tracking turtle ID 12545, it is possible to observe that both edges and center of a cold-core eddy were occupied, although a high amount of ARS locations occurred in the center of a cold-core-eddy (FIGURE 10).

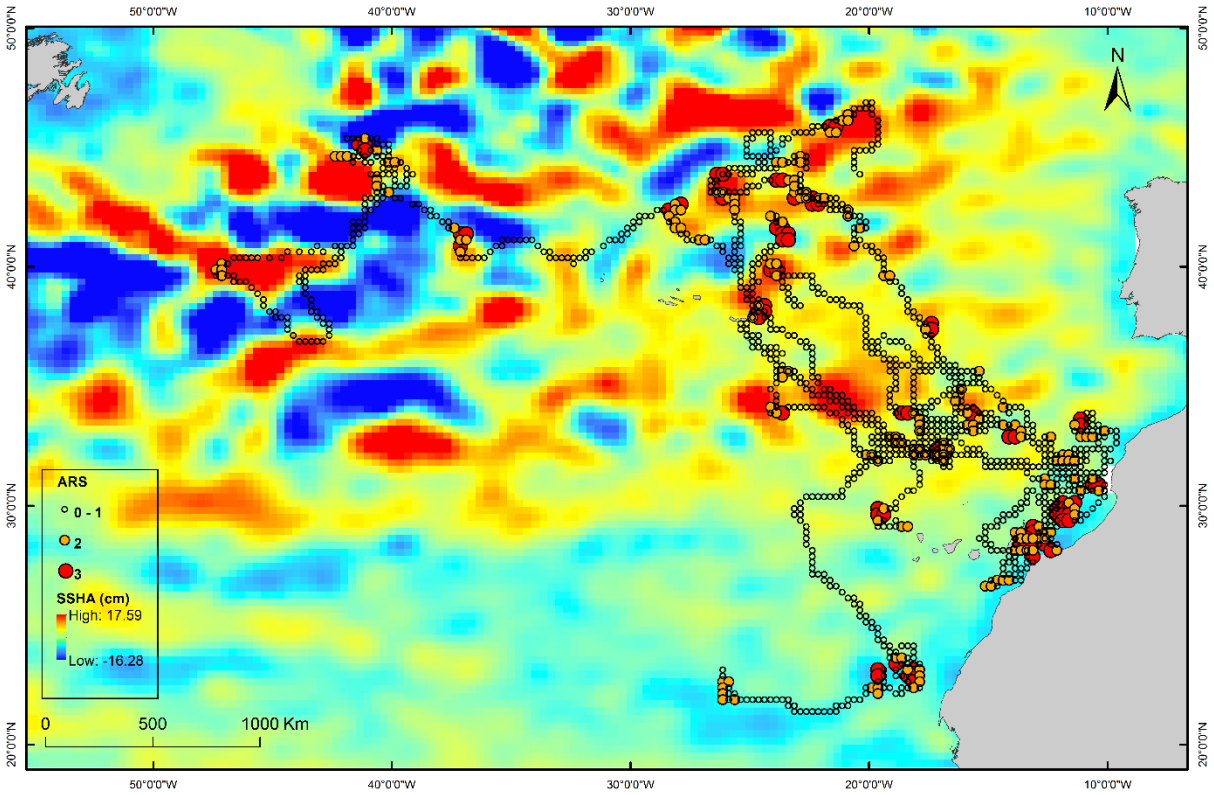

FIGURE 9 - ARS results plotted over a cumulative SSHA gridded map (larger image available in APPENDIX I, FIGURE 22).

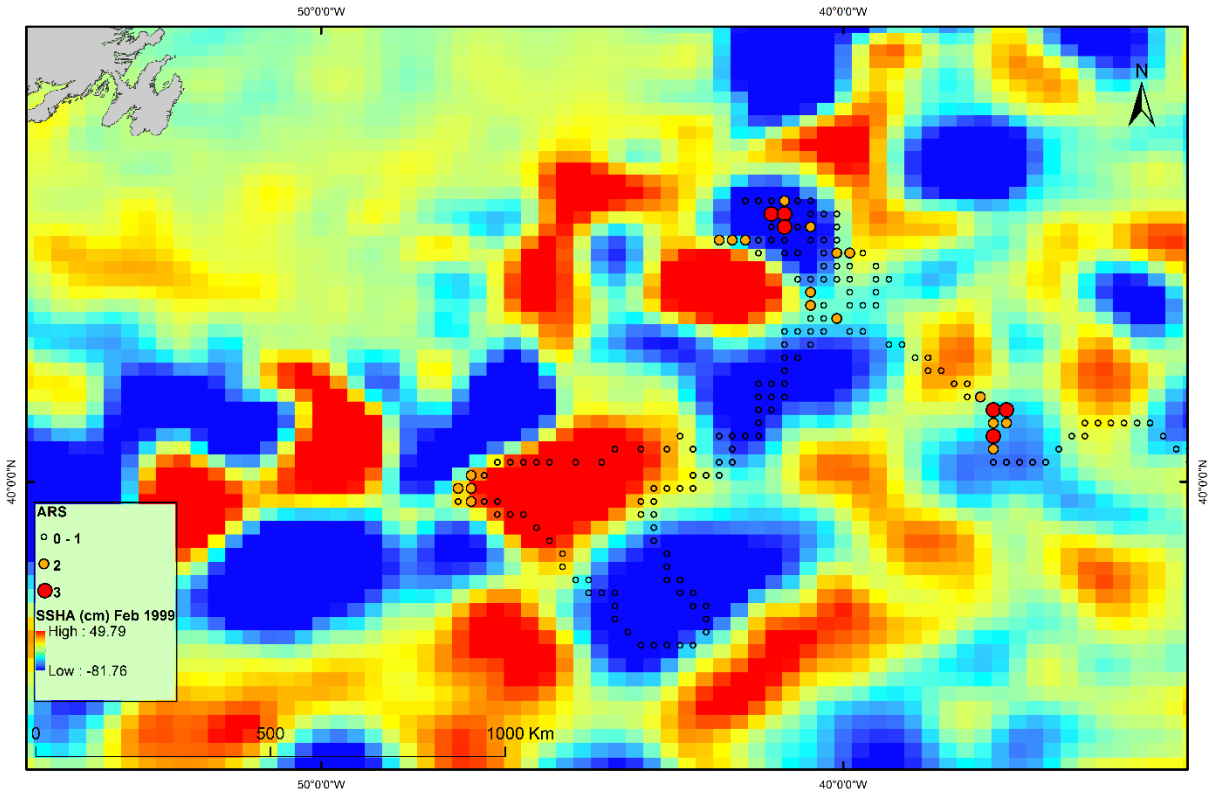

FIGURE 10 - ARS detail map for turtle ID 12545 plotted over February 1999 SSHA gridded map (larger image available in APPENDIX I, FIGURE 23).

3.2.2.5 - Chlorophyll *a* (Chl*a*):

The 10 turtles travelled within ranges of [Chl*a*] of 0.027-15.61 mg/m^3, with an average [Chl*a*] of 0.27 mg/m^3. For ARS=1 locations, the mean [Chl*a*] value is higher (0.325 mg/m^3) (see APENDIX III, TABLE 1). As for log-transformed [Chl*a*], the mean value was -1.87, within a range from -3.62 to 2.74. Mean value and ranges for ARS=1 locations were slightly lower, as mean log transformed [Chl*a*] was -1.65 and values ranged from -3.24 to 2.19.

Considering mean [Chl*a*] variability within each season (TABLE 11), it is possible to observe that the higher values for [Chl*a*] occurred during winter, as summer and autumn were the seasons with lower values for this variable.

TABLE 11 - [chl*a*] ranges during seasons for all the 10 turtles.

		spring	summer	autumn	winter
Chl*a* (mg/m3)	Min	0.07	0.03	0.03	0.12
	Max	3.89	0.62	0.53	4.82

By plotting ARS over a cumulative mean gridded [Chl*a*] map (FIGURE 11), it is possible to visualize that the region with the higher [Chl*a*] is located near the African coast, where a high amount of ARS locations also occurred. Autumn-tagged turtles IDs 12007, 12570, 12571 and spring-tagged turtle ID 12547 remained in this area for several months, during winter 1998 and spring 1999 (ID 12571 remained in this region for about 7 months, from November 1998 until June 1999). Although most of these turtles used the same area, one of them (ID 12570) headed towards lower latitudes, remaining for about 3 months (from February to April 1999) within a near-coastal high [Chl*a*] region, which is coincident with the higher number of ARS locations for this turtle.

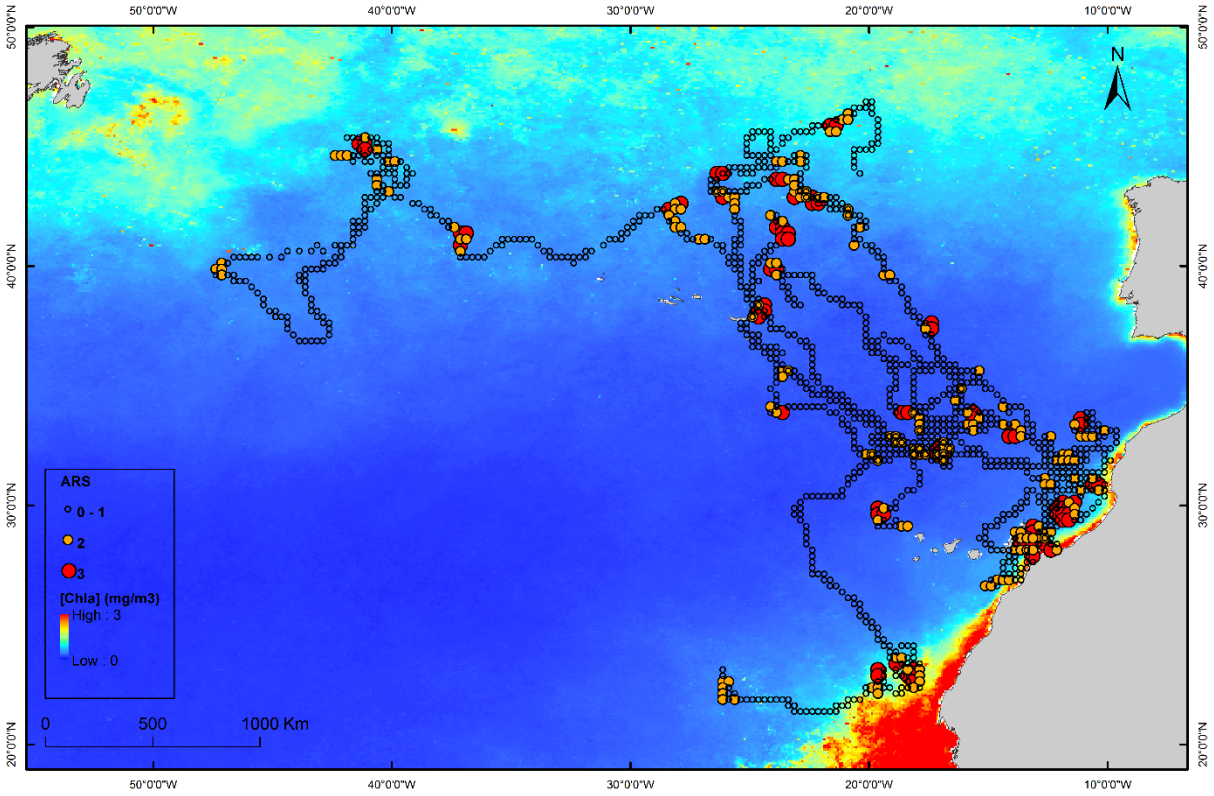

FIGURE 11 - ARS plotted over SeaWiFS cumulative [Chl*a*] gridded map (larger image available in APPENDIX I, FIGURE 27).

Although there is a visual relation between ARS and Chl*a* for these turtles, it is possible to observe that most of the ARS locations do not match the highest [Chl*a*] values but, instead, occur within the boundaries of higher and lower [Chl*a*] values (FIGURE 12). The same pattern is found for some of the turtles that travelled north, IDs 12538 and 12544, as both turtles spent the last tracked months (November and December 1998) within the boundaries of low and high [Chl*a*], and also for turtle ID 12545, at the Flemish Cap, during winter 1998 (detail maps available in APPENDIX I, FIGURES 28 and 29).

By plotting ARS over a log-transformed gridded Chl*a* map (FIGURE 13), it is possible to observe a pattern between the turtles' higher and lower latitudes limits and the boundaries between low and high [Chl*a*].

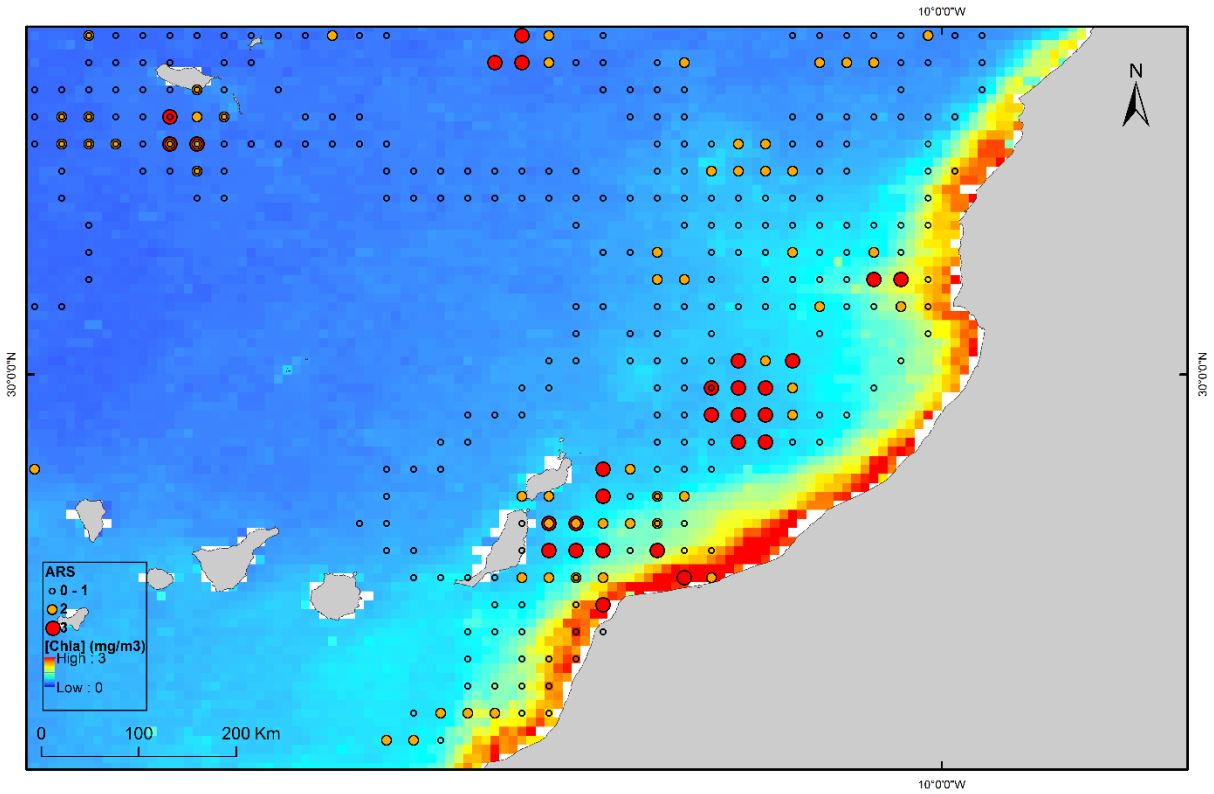

FIGURE 12 - Detail ARS map for turtles IDs 12007, 12570 and 12571 plotted over SeaWiFS cumulative [Chl*a*] gridded map.

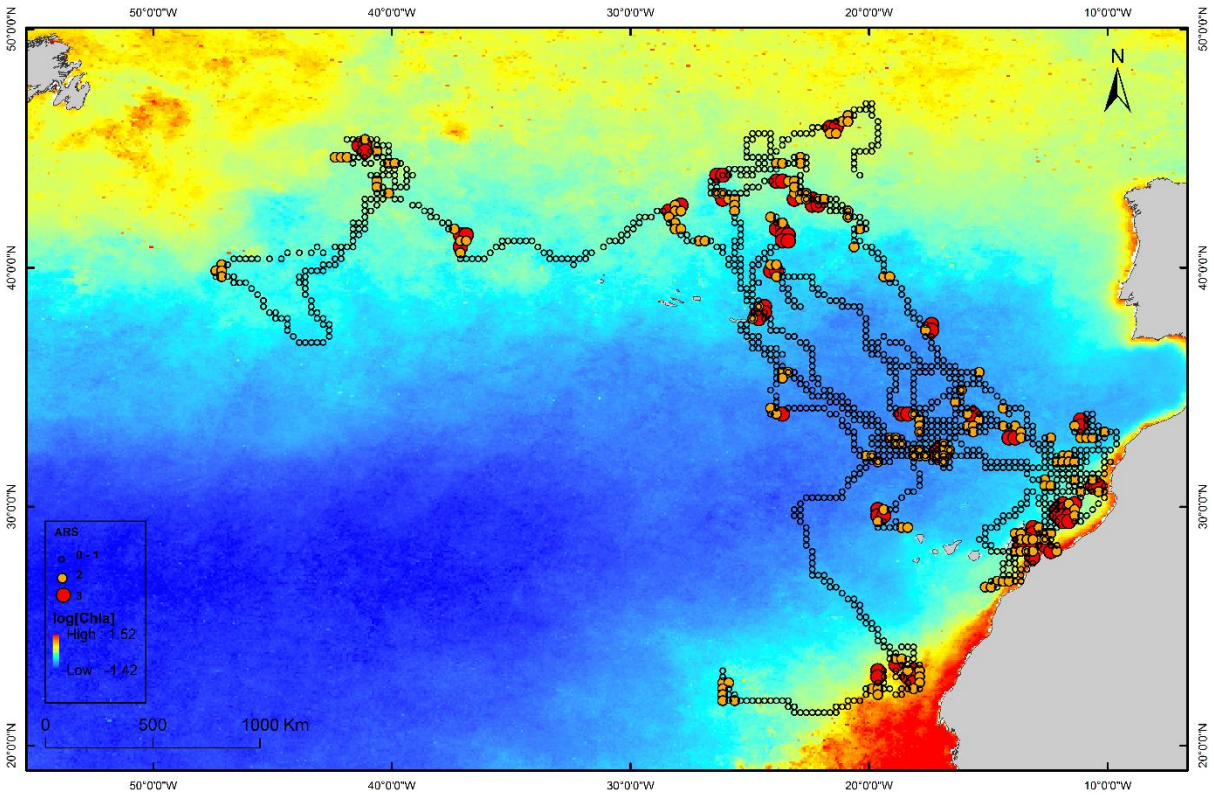

FIGURE 13 - ARS plotted over SeaWiFS cumulative log-transformed [Chla] gridded map (larger image available in APPENDIX I, FIGURE 30)

3.2.3 – ARS density histograms:

Density histograms for the environmental variables in relation to ARS=0 and ARS=1 locations (APPENDIX IV, FIGURE 32) have shown that there are some differences in ranges of non-foraging and foraging locations higher densities, for some of the environmental variables. For bathymetry, the higher density of non-foraging regions occurs within higher bathymetry values than for foraging locations. Foraging locations have their higher density (peak) within values around -3500 m (and another peak at around -2000 m), while non-foraging regions have higher density at around -4500 m. For SST, higher density of foraging locations occurs within lower values of SST, in relation to non-foraging locations. For this variable, foraging peak density occurs at around 18^0C, while in these lower temperatures the density of non-foraging locations is considerably lower, and the opposite occurs at higher temperatures, where non-foraging locations density has its peak around 24^0C, while a decreasing foraging locations density is visible. For log-transformed Chl*a*, foraging locations occur within a displacement of slightly higher values, corresponding to higher [Chl*a*] values. The higher density of non-foraging locations (peak) occurs at around -2.6 (0.07 mg/m^3), while the higher density of foraging locations (peak) is around -2.1 (0.12 mg/m^3). There is another peak for both foraging and non-foraging locations (although with higher densities for foraging locations) at around -1.2 (0.30 mg/m^3).

For the other variables, there is not a clear different pattern observed between foraging and non-foraging locations density, and higher density of both foraging and non-foraging locations for SSH occurs at around 20 cm, and for SSHA occurs closer to 0.

3.3 – Generalised additive model (GAM) results:

3.3.1 – Variables correlation:

For general comparison, a model containing all variables was produced, and also models concerning individual predictors were also fitted to the training data. Pearson's correlation coefficients (APPENDIX V, FIGURE 33) have shown the existence of a strong correlation (>0.60) between SST and both SSH (0.65) and log-transformed Chl*a* (0.68). Since the coefficient obtained for the correlation between SSH and bathymetry was 0.59 (very close to the 0.60 threshold), models without both variables were also fitted to the data. Therefore, different models were produced, having into account the non-inclusion of strongly correlated variables in the same model.

3.3.2 – GAM results:

According to the output values obtained for the models that didn't contain highly correlated variables, UBRE (Un-biased Risk Estimator) scores for all models were very similar (TABLE 12). The chosen best fit model was model D, as this presented the lower UBRE score (-0.033) and higher deviance explained (9.55%). This model contains all variables except SST. The AUC obtained while performing model validation was also the highest (0.712) for model D, which means that the model was the one with the best adjustment to the data, in relation to all other models which contained non-correlated variables. The automatic cutoff selected by maximizing the Youden Index obtained was 0.241 (see APPENDIX VI for more details).

TABLE 12 - GAMs produced and respective output values of the deviance explained, UBRE score and AUC. (*) – Models containing the non-correlated predictors (A, B, C, D).

Formula	Deviance explained	UBRE score	AUC
ARS= s(SST)	2.20%	0.01866	0.608
ARS= s(SSH)	3.47%	0.01084	0.615
ARS= s(|sshA|)	2.46%	0.02181	0.597
ARS= s(log(Chl*a*))	4.02%	0.00438	0.627
ARS= s(Bathymetry)	2.14%	0.02335	0.598
ARS = s(SST)+s(SSH) + s(|sshA|) + s(log(Chl*a*)) + s(Bathymetry)	11.70%	-0.04843	0.722
A: ARS= s(SST) + s(|sshA|) + s(Bathymetry) **(*)**	6.40%	-0.01128	0.650
B: ARS= s(SSH) + s(|sshA|) + s(log(Chl*a*)) **(*)**	8.49%	-0.02801	0.687
C: ARS = s(|sshA|) + s(log(Chl*a*)) + s(Bathymetry) **(*)**	7.61%	-0.02010	0.678
D: ARS= s(SSH) + s(|sshA|) + s(log(Chl*a*)) + s(Bathymetry) (*)	**9.55%**	-0.03342	0.712

Formula of model D was then applied to the entire dataset. So, the final formula is:

ARS= s(SSH) + s(|SSHA|) + s(log [Chl*a*]) + s(Bathymetry)

All predictor variables within the model have shown to be significant (TABLE 13).The significance order of the smooth terms (p-value) is: s(|sshA|) (3.17e-12) > s(ssh) (5.34e-11) > s(log [Chl*a*]) (1.60e-11) > s(bathymetry) (2.06e-6) and the deviance explained for the data was 9.5% (n = 3202).

By analysing each smooth term plot individually (FIGURE 14), it is possible to observe that, for predictor SSHA, ARS is positively influenced by higher absolute values of sea surface height anomalies (values roughly above 11 cm). As for sea surface height, ARS exists within 3 different intervals (0-10 cm, 18-25 cm and 32-45 cm). Log [Chl*a*] smooth term plot shows a distinctive region of ARS occurrence within values around -2.5 and -1.8, which correspond to

[Chl*a*] values between 0.081 mg/m^3 and 0.165 mg/m^3. For this predictor, ARS also is positively influenced by log [Chl*a*] values closer to 1, especially values above 0.5, which correspond to [Chl*a*] values above 1.650 mg/m^3. Bathymetry smooth plot shows ARS occurring in intervals [-4000,-3000 m], [-2300,-1000 m] and also close to 0 m.

TABLE 13 - Approximate significance of smooth terms for GAM applied to the entire dataset

Variable	edf	Ref.df	Chi.sq	p-value
s(ssh)	7.489	7.923	64.59	5.34e-11 ***
s(abs_sshA)	7.804	7.987	70.93	3.17e-12 ***
s(log_chl*a*)	7.974	8.589	68.88	1.60e-11 ***
s(bathymetry)	7.642	8.523	42.13	2.06e-06 ***
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1				

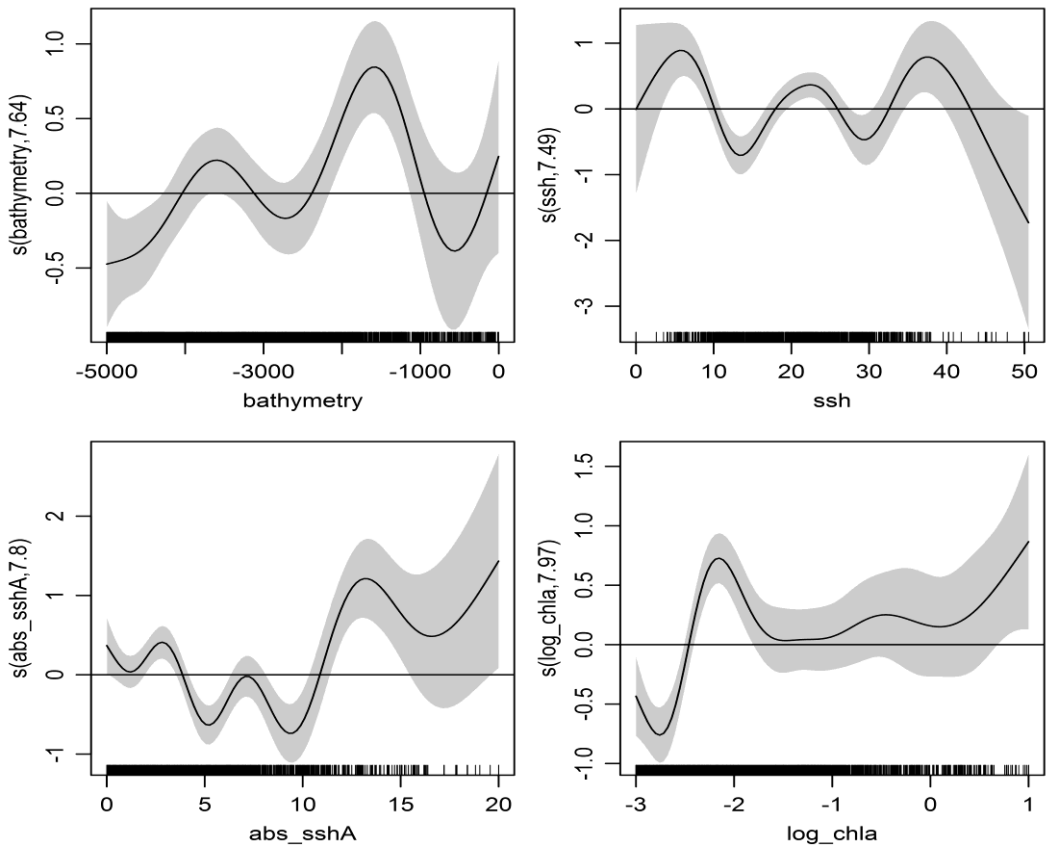

FIGURE 14 - Output plots for GAM smooth terms; estimated smooth functions (solid line) with 95% confidence interval (shadowed region) are shown for each explanatory variable; y-axis=fitted function with estimated degrees of freedom in parenthesis; x-axis=variable range with rug plots indicating variables' values

4 - DISCUSSION

4.1 - Movement patterns:

The turtles were tracked from three months to almost a year, allowing the identification of likely foraging regions, represented as ARS locations, and an interesting relation with the existing environmental variables within their oceanic habitat.

In terms of space use, there was a clear divergence in the initial headings of spring-tagged and autumn-tagged turtles and only two of the ten animals did not follow the exact same initial pattern of the other turtles that were tagged in the same season. Most of the spring-tagged turtles headed NW from the release point, and most of the autumn-tagged turtles headed SE, possibly traveling to latitudes that would match comfortable temperatures, as it has been seen in other studies, where oceanic juvenile loggerheads performed seasonal migrations in order to remain in waters between 17^{0}C and 20^{0}C (Avens et al. 2003, Polovina et al. 2004, Hawkes et al. 2011, Casale et al. 2012). Seasonal distributions were also found by Arendt et al. (2012b), in the Northwest Atlantic, when loggerheads returned to foraging grounds that they have occupied the previous same season. These authors also refer that the animals inhabited regions with a slightly higher temperature in warm seasons and lower temperature in cold seasons, which also occurred in the present study, as winter temperatures were lower than in warm seasons. This pattern was also observed by Abecassis et al. (2013), in the North Pacific, where loggerheads remained in a narrow range of temperature (16.7-17.5^{0}C) in the winter, and within slightly higher temperatures in the summer (19-21^{0}C). However, loggerheads from the present study occupied areas within larger temperature ranges, particularly during winter (12.5-21.5^{0}C), and a slightly smaller range during summer (17.6-24.8^{0}C), due mostly to turtle ID 12545, as in winter this animal occupied colder regions, close to the boundary of Labrador and Gulf currents. The slight difference found between turtles' temperature ranges in this study in relation to others may be due to the fact that some of these turtles occupied almost opposite latitudes within the same season (some turtles spent the winter close to the African coast while other turtle was in the Flemish Cap, which is a considerable range in latitude (and hence, in temperature) within a single season). However, in general, they headed towards opposite regions depending if they had been released in spring or autumn, and these headings were consistent with temperature changes along seasons, which could mean that, in a large scale, the animals travel to maintain within a comfortable temperature range. This seasonality was also consistent with [Chl*a*] values, which were higher in winter and lower in summer. Some of the turtles concentrated in the region

near the African coast during the entire winter, where [Chl*a*] was found to have the higher values, while others spent winter within higher latitude regions, which also had higher [Chl*a*] than the mid latitude regions the turtles occupied during summer. In general, latitude ranges obtained for the tagged turtles were consistent with global ranging for these animals, as studies from different regions provided identical ranges (Polovina et al. 2001, Kobayashi et al. 2008). A relation between nesting and migration latitudes has been found (Monzón-Argüello et al. 2009), as turtles that are born in lower latitudes (e.g. Western South Atlantic) migrate to Eastern Atlantic regions within the same latitudes, and turtles born in higher latitudes migrate within those same higher latitudes. Therefore, the tracked turtles were most probably born in southeastern USA nesting beaches (northwest Atlantic) (Bolten et al. 1998, Delgado et al. 2011), as the occupied latitudes are consistent with these nesting sites, although it is also possible that some juveniles were originated from Cape Verde, as it has been seen that some mixture of both populations may occur in the same oceanic regions (Conant 2009). The two not completely matching patterns that were found when analysing latitude ranges within seasons may be due to the fact that one of the turtles tagged in each season evidenced a different direction in relation to the other turtles (spring-tagged ID 12547 travelled to lower latitudes and autumn-tagged ID 12573 travelled to higher latitudes). Moreover, there is a large difference between the elapsed time of tracking for the turtles (from 58 days to 342 days), which may also be responsible for the resulting slightly different patterns.

It is well documented the homing behaviour of female loggerheads in relation to their nesting beaches, returning from long migrations to the place where they were born, to lay their eggs (Conant et al. 2009). Also adult loggerheads have been found to show fidelity to their neritic feeding grounds (Broderick et al. 2007, Schofield et al. 2010a, Casale et al. 2012). In this work, one of the autumn-tagged turtles, ID 12571, after spending about roughly 8 months (November-June) off the coast of Morocco, headed NW and quickly reached the waters of Madeira again (in August), appearing to present fidelity to that foraging ground. This foraging fidelity behaviour was also found by (Casale et al. 2012), who mention strong fidelity to specific foraging areas by juvenile loggerheads in the Mediterranean. Also (Rees et al. 2013) mention the site fidelity of juvenile loggerheads to their oceanic feeding areas. Another possible reason for this turtle to have headed almost straightforward to Madeira after spending a long time foraging off the African coast is the chance of having found a current, which probably occurred, as it is possible to observe increasing speed and distance travelled during that time (as in other portions of other turtles' paths). McCarthy et al. (2010), when analysing these turtles, found that the animals swimming with the prevailing geostrophic current are more likely to have straight tracks, and this is consistent with the visible straighter paths' portions, where higher speed and longer distances travelled within short periods of time were found. Since this

turtle started to head north right after reaching Madeira, but then transmissions stopped, there is also the possibility that these islands may also function as orientation cues for these animals, further than being foraging grounds.

Although the tracked animals were juveniles, results show that they had the ability to travel along, against or perpendicularly to the currents. This fact was confirmed by the plots of the resulted angles between turtles' bearings and currents' directions, in which, for most of the turtles' locations, the angles to current corresponded to 90^0, meaning that most of the time, they were not travelling against the currents nor taking advantage of them. This was also found by Polovina et al. (2006), where juvenile loggerheads in the North Pacific moved independently of the currents' strength and direction, with some of the turtles seeing their movements reduced by 50% by the opposing current, while others, that swam with the currents, exhibited an increase in directed zonal movement, meaning that, although currents influence their velocity and displacement, these animals are clearly not passive drifters in a major ocean. Although turtles' velocities were corrected with the currents directions and magnitudes, the fact that most of the time they were performing a 90^0 angle to current may be somewhat one of the reasons they headed NW instead of North, as it has been seen that lateral currents may deflect turtles from the optimal route towards their target, displacing them sideways (Luschi et al. 2003).

4.2 - Foraging areas and environmental variables

It is known that post-hatchling loggerheads originated from the coast of the southeastern United States are carried by the North Atlantic gyre to the Azores and past Madeira and the Canary Islands, before returning to western Atlantic waters (Bolten et al. 1998). Moreover, there is a juvenile population of loggerheads inhabiting the waters offshore Madeira (Delgado et al. 2011), spending time in these waters as they carry their growing migration. However, the high amount of ARS locations obtained near Madeira, short after the release date, may be biased by the fact that these turtles were kept in captivity for about a week, previously to the release, and may have been spending more time in that region after being released, while they were getting adjusted to the "new" environment, before performing a seasonal migration.

ARS results have shown one large foraging region, near the African coast, where some of the turtles spent most of their tracked time, highlighting the ecological value of this region, which is consistent with the fact that this coastal area holds a persistent upwelling, and may provide feeding habitat for many species throughout the year. Palacios et al. (2006) also highlighted the significance of seasonal coastal upwelling, as it may lead to predictable development of foraging regions year after year, and many marine species have evolved to

synchronize their life cycles with the presence of these persistent features. By analysing the oceanographic variables for this region, both low bathymetry values and high [Chl*a*] were found, confirming that these are important parameters to consider when determining possible important foraging regions to preserve. These variables have also been found meaningful in other studies related with loggerheads' foraging environment (Polovina et al. 2000, Kobayashi et al. 2008) and also with other species (Mugo et al. 2010, Dalla Rosa et al. 2012, JA et al. 2012, Weltz et al. 2013, Farrell et al. 2014, McClellan et al. 2014). When analysing the same turtles as the present study, McCarthy et al. (2010) also found that both bathymetry and [Chl*a*] were related with the turtles' higher sinuosity tracks segments. Another meaningful low bathymetry region was Newfoundland Basin, which was one of the main ARS regions for turtle ID 12545. This region is a foraging ground for a mixture of loggerheads from all the North Atlantic rookeries (Bowen et al. 2005). According to Kobayashi et al. (2008), bathymetry has shown to be a better descriptor when examining coastal behaviour and not very useful as habitat characterisation of loggerheads' pelagic habitat, where other variables, like sea surface height related features, shown to be better descriptors. Results in the present study for this region have shown that not only bathymetry was a major feature in Newfoundland Basin, as results for sea surface height anomalies showed the presence of both warm-core (clockwise movement) and cold-core (counter-clockwise movement) mesoscale eddies. Most of the ARS locations for the turtle that headed for this region occurred particularly in the Flemish Cap region. This region is located within an area of transition between the cold waters of the Labrador Current and warmer waters influenced by the Gulf Stream and the mixing of the warm and cold waters over the plateau produces the characteristic semi-permanent anticyclonic gyre (warm-core) circulation current over the cap (Hendrickson et al. 2005).

The importance of cold-core eddies as foraging open ocean areas for many species has been already documented (Polovina et al. 2004, Polovina et al. 2006). According to these authors, the counter-clockwise circulation that occurs in these cold-core eddies creates upwelling at the center and convergence at the edge, where the buoyant prey of loggerheads most likely concentrates. Their results showed that loggerheads occupied the edge of these features for months. However, the same authors found that the turtles also occupied the edges of warm-core eddies, although in these features the upwelling occurs in the edges and convergence in the center. The explanation found was that subsurface prey was concentrated at shallow depths at the edge and more accessible to the shallow-foraging loggerheads. Results in present study are consistent with these findings, which is quite visible for turtle ID 12545, as this turtle remained for about 3 months foraging within both cold-core and warm-core eddies, although ARS locations occurred in both edges and center of these features. However, for warm-core eddies, it is more visible the presence of the turtle at the edges, and

in cold-core eddies, most foraging locations occur in the center, which the opposite of what would be expected. The lack of environmental data within several locations in this and other regions may be possibly masking different results, because there are several locations along the turtles' paths for which there were no environmental data available for some predictors (particularly Chl*a*). For the remaining turtles' paths, the presence of warm-core eddies prevailed in the regions occupied by them, and is possible to see many ARS regions perfectly matching the edges of existing warm-core eddies. A fine-scale analysis of these events, including both more accurate locations data, information about diving activity and environmental data at depth, would possibly provide information that would help to clarify the interaction between turtles and eddies, as possible subsurface movements could be related with other specific events within the eddy, such as nutrient flow or thermocline displacement (in warm-core eddies, the thermocline is pushed downwards and the surface is slightly raised, and in cold-core eddies, the opposite occurs) (Nencioli et al. 2008). This feature was also highlighted by Schick et al. (2013), while studying foraging behaviour of leatherback turtles (*Dermochelys coriacea),* who mentioned that the presence of the thermocline or halocline at depth might be a patterning variable for jellyfish, and turtles might respond to it rather than some other surface variables (like temperature). Although loggerheads usually spend more time at the surface than leatherbacks, it is possible that subsurface features may be playing some more important roles within their foraging behaviour. GAM results were consistent with the visual usage of eddies, both cold and warm-core eddies, by the turtles, as ARS was related with both lower and higher sea surface height anomalies. In fact, |SSHA| was the most significant predictor for foraging regions, and this was also visible in the variable plot, where foraging locations mostly occurred within the higher absolute values of sea surface height anomalies. The importance of mesoscale eddies has also been highlighted by TK et al. (2008), when studying the behaviour of a leatherback turtle tagged in the Irish Sea. The animal remained for several months within a mesoscale eddy in the Bay of Biscay Region, suggesting the existence of good foraging conditions. In fact, it is expected that in the middle of the ocean, where resources are scarce, these kind of formations, capable of providing food to higher trophic level organisms due to upwelling forces, would be regions where a higher concentration of animals of many species would occur, as documented by many authors (Polovina et al. 2006, Revelles et al. 2007, Godø et al. 2012, Farrell et al. 2014).

Another interesting feature is the one presented in the turtles' latitudes limits, where foraging occurs in visible sea surface temperature front, where is possible to see the boundary between higher and lower temperatures, particularly in the tracks' higher latitude limits, where a sharp sea surface temperature change exists and the animals' foraging locations occur between the limits of low and high temperatures. These findings are consistent with the ones

obtained by Kobayashi et al. (2008) and also in studies with other species (Nieblas et al. , Mugo et al. 2010). Although SST was not included in the final model, due to the fact that it was strongly correlated with other predictors (SSH and log-transformed [Chl*a*]), GAM plots for SST showed that this predictor positively influences foraging locations in values between 16^0C and 22^0C, which is also consistent with foraging SST ranges found in other studies (Polovina et al. 2004, Hawkes et al. 2011). Also the density plot for this variable was consistent with these results, as temperature range for higher density of ARS locations was between 17^0C and 21^0C, with a peak at around 18^0C, while non-foraging regions occurred mostly at higher temperatures, which would be expected, since most foraging regions are usually associated with upwelling forces that bring colder, rich nutrient waters to the surface, providing foraging habitat for an entire trophic cascade (Baylis et al. 2008).

The turtles were also visually related with Chl*a* higher concentrations and, especially, Chl*a* fronts, as the animals' foraging regions in their higher and lower latitudes' limits match intermediate values of [Chl*a*]. This relation relationship corroborates the findings of Polovina et al. (2000, 2001, 2004), when tracking the movements of loggerheads in the North Pacific, and their results indicated that oceanic fronts, particularly the chlorophyll *a* front known as the Transition Zone Chlorophyll Front (TZCF), provided mid-oceanic forage and migration habitat for these juvenile loggerheads. The TZCF represents the boundary between the stratified low surface chlorophyll *a* (<0.15 mg m^3) waters of the Subtropical Gyre and the high surface chlorophyll *a* (>0.3 mg m^3) vertically mixed waters in the Transition Zone and Subarctic Gyre (Polovina et al. 2004), and these authors found that the turtles were mostly foraging within these boundaries, particularly within [Chl*a*] values of 0.1–0.3 mg/m^3. This is consistent with the present study, as visually, the turtles foraging regions in relation to [Chl*a*] are distributed mainly within mid values, and not only where [Chl*a*] is higher, which was also confirmed by the GAM results, as the log-transformed [Chl*a*] variable was highly significant in relation to ARS locations, and was particularly visible a peak in this variable plot where ARS locations are mostly concentrated within corresponding values of [Chl*a*] from 0.081 mg/m^3 to 0.165 mg/m^3. Density plot for this variable has also shown a higher density of ARS locations within values around 0.07 mg/m^3 and another smaller peak corresponding to values around 0.3 mg/m^3, which is almost exactly the same range of values found by Polovina et al. (2000). A possible explanation for the higher number of foraging locations within these intermediate values of [Chl*a*] is that loggerheads' prey would most likely be concentrated in these fronts, as they correspond to convergence zones between cool plankton-rich and nutrient-poor waters, as it was documented by Polovina et al. (2000). Dalla Rosa et al. (2012) also highlight the possibility of phytoplankton being drifted away from the producing area by wind, currents and eddies, which could explain the fact that foraging regions match mostly these areas

slightly away from the higher productivity regions. The same authors also refer that there may be higher phytoplankton concentrations at intermediate depths if vertical mixing is not strong enough, which would not be detected by satellite sensors scanning surface waters. A Fine-scale analyses with higher spatial resolution and also diving and depth environmental data would possibly allow a better understanding of this relationship between the animals foraging preferences and [Chl*a*] values.

4.3 - General conclusions

In general, results have shown that the animals tend to travel within latitudes that correspond to comfortable temperature ranges, taking advantage of geostrophic currents as long as they provide them means to travel to or remain within a suitable forage habitat or perform migrations, but not totally depending on them to choose foraging sites. Also, the animals foraged in regions where one or more of these features occurred: low bathymetry, higher positive and negative sea surface height anomalies and also within the boundaries of sea surface temperature fronts and [Chl*a*] fronts, as these are regions where their prey availability is probably higher, due to the upwelling forces that occur, bringing to the surface more resources. McCarthy et al. (2010), when examining the relation between sinuosity and environmental variables for the same turtles, mentioned that low bathymetry, higher SST and chlorophyll *a* gradient values were found to have a link with more sinuous paths. Results in the present study are consistent with these results and have also shown that other features may be playing an important role when analysing juvenile loggerheads' foraging behaviour, particularly sea surface height anomalies, as it has been observed that these formations perfectly match foraging regions and |SSHA| was also a significant predictor in the model.

Although it's easy to visually relate specific foraging regions with one or more environmental variables, almost giving the impression that it would be possible to characterise foraging regions by using only that one single variable, each variable by its own probably wouldn't be able to predict alone many other foraging regions. For instance, some foraging areas occur in regions where [Chl*a*] values are low or there is no available data, so these areas wouldn't even be considered if only [Chl*a*] had been used to characterise the turtles' oceanic habitat. Therefore, it would be prudent to always have into account several environmental predictors to identify possible foraging regions, as their combination results better. However, it is also clear that for most regions, these variables are related, as coastal low bathymetry areas usually have higher [Chl*a*], and regions where upwelling is occurring brings cold rich nutrient water to the surface, therefore sea surface temperature in that area is lower and [Chl*a*] is higher. This means that, although most variables were not found to be

strongly correlated, they are not completely independent, which may raise a question when producing statistical analysis. GAM results corroborated most of the visual results, as all the environmental variables within the model were highly significant in relation to ARS=1 locations. Although GAMs are capable of dealing with highly nonlinear and non-monotonic relationships, being ideal for expressing relationships in ecological systems (Mugo et al. 2010), the model would probably benefit of more improvements, as it is possible that some overfitting has occurred, and also all the attempts (except with excessive number of knots) failed to obtain higher deviance explained and higher AUC, meaning that the model didn't quite succeeded in truly explaining the results or greatly adjusting to them. Nevertheless, the main objective of using GAMs in this work was achieved, as the model was capable of expressing the existing relation between several environmental parameters and foraging areas, and showing how that relation is occurring, by analysing the trends of the smooth functions.

The combination of three methods to determine ARS showed to be more restrictive than the use of exclusively one, as it was visible by plotting ARS determined by each different method. In fact, the preliminary results obtained by considering each method independently revealed a great amount of common foraging areas, but also some exclusive ones. On the other hand, if more than one method has considered a certain location as foraging location, it probably means that the location is indeed a foraging one. Moreover, the combination of these methods allowed building a scale and discriminate ARS regions where 0-1, 2 or 3 methods were in agreement, which revealed to be useful to recognize major foraging regions (for instance, the region offshore the African coast). Tancell et al. (2013) mention that the application of several relatively simple methods based on different assumptions revealed more ecological insight than a single complex method and provided a robust analytical technique that could be applied to large datasets and different species to help identify key marine areas.

Although results have shown that the combination of the methods applied allowed the detection of large-scale foraging regions, possibly some more information could be provided if tracking methods with higher resolution could have been applied, especially when considering fine-scale regions, as ARGOS errors are relatively high and may be somewhat deceiving. This has also been highlighted by Mencacci et al. (2010), who mention that tracking would take advantage of more accurate route reconstruction, using, for instance, GPS system. This information could be important, for example, to confirm the use of the edges or the center of both warm-core and cold-core eddies, because although some of these features are relatively large, it is not always easy to clearly understand which region of the eddy the turtle is using.

In future studies, assembling information provided by different and complementary methods will most likely provide a deeper knowledge of loggerheads' foraging ecology. One

of these complementary methods that could be used to enhance this study would be stable isotopes analyses, as it would become possible to understand if, for instance, the animals were all originated from the same region or if they were a mixture of more than one population, as it has been observed that Cape Verde juvenile population also may inhabit the same oceanic habitats (Conant et al. 2009), which could be used to compare with the animals' behaviour (space use or directions they headed).

A stomach content analysis could also have been helpful to confirm these turtles' preferences, as much is still unknown in relation to oceanic juvenile loggerheads feeding habits (COSEWIC 2010).

Information about diving activity would possibly help to complement foraging data and also investigate the epi-pelagic habitat of these specific animals, as it has been documented in other studies, which would confirm that using sea surface environmental data is suitable for analysing the turtles' environment. Diving data and environmental conditions at the animals' depth would also help to reveal some possibly hidden information about the use of SST and Chl*a* fronts, and specific possible features within eddies, and would also enable to relate changes in thermocline depth with the animals' activity. Also information about resting periods could be helpful to possibly eliminate some locations that were previously considered as foraging ones, as some of the parameters used (time spent in a certain area) may be biased by resting periods. However, since the turtles' interpolated positions have a 12h time-step, any resting period wouldn't probably make any difference, as it has been seen that loggerheads longer resting periods occur only for some hours (Hays 2008).

Although there are not visible morphological differences between genders in juvenile stages, information about the animals gender could also have been useful to complement this study, by analysing the sex-ratio and possible differences observed between the behaviour of males and females, which would have been possible by obtaining blood samples from the animals. The same way, although loggerheads inhabiting Madeira waters are juveniles, and therefore, their sizes are probably similar, information about the turtles' sizes and weights could have been useful to compare with distances travelled, velocities achieved and their ability to deal with the currents.

While some predictive models concerning loggerheads' habitat use and interactions with fisheries have already been made (Warden 2011, Hart et al. 2013), more studies focusing oceanic stages of these animals are needed, as many aspects of their foraging habits are still not completely understood. Marine turtles spend the larger portion of their lives between migrations and foraging grounds. Consequently, it is important not to limit any analysis upon marine turtles to breeding sites (Mazaris et al. 2009).

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APPENDICES

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(All images are also available in higher resolution on digital format, within the folder "IMAGES APPENDICES")

APPENDIX I – Maps

A – Turtles' movements

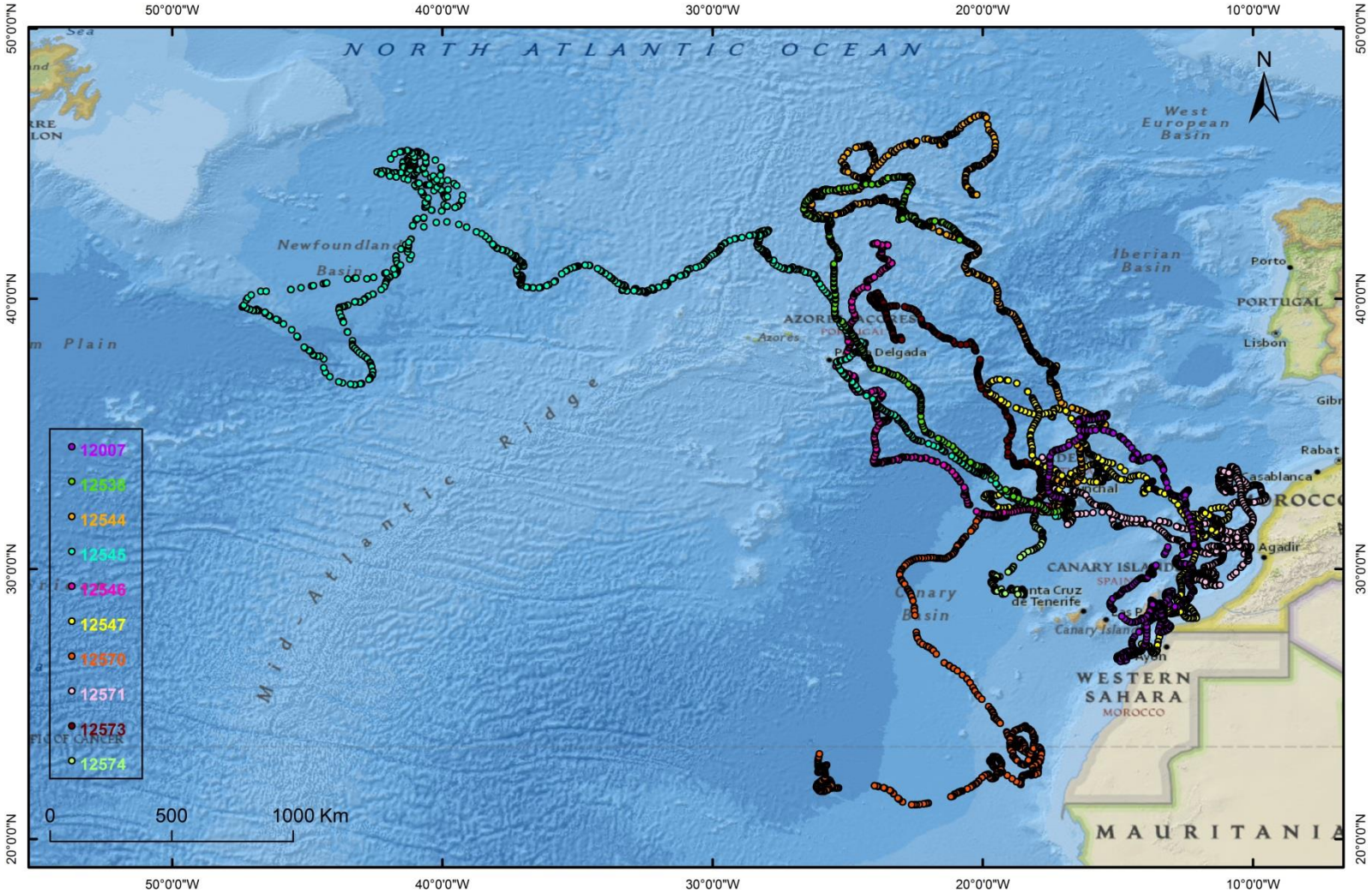


FIGURE 1 – General visualization of the turtles' tracks (original positions corrected with SSM-KF) plotted over National Geographic Basemap (available in ArcMap™ (ESRI 2011))

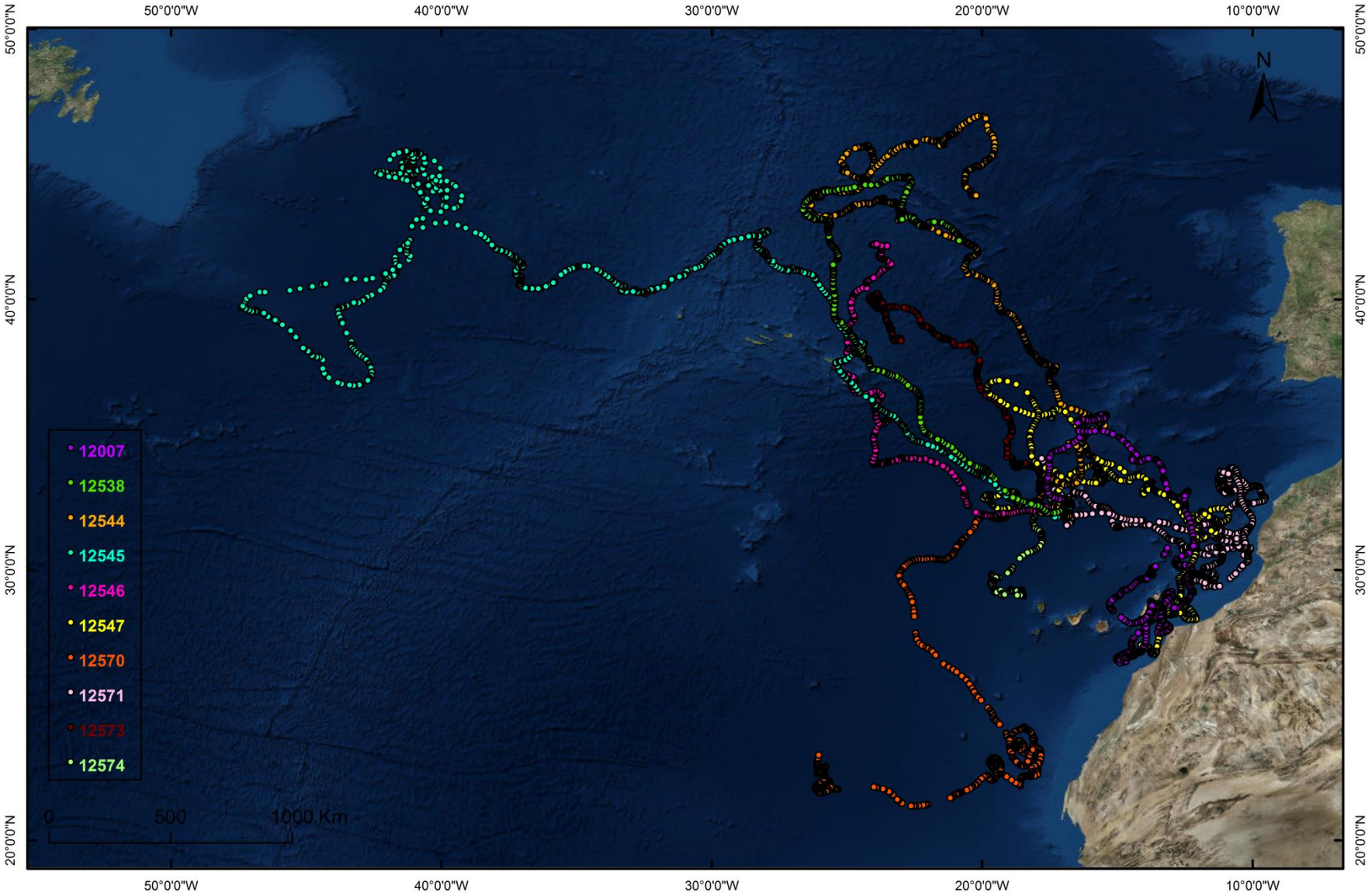


FIGURE 2 – General visualization of the turtles' tracks (original positions corrected with SSM-KF) plotted over Google Earth Basemap (available in ArcMap™ (ESRI 2011))

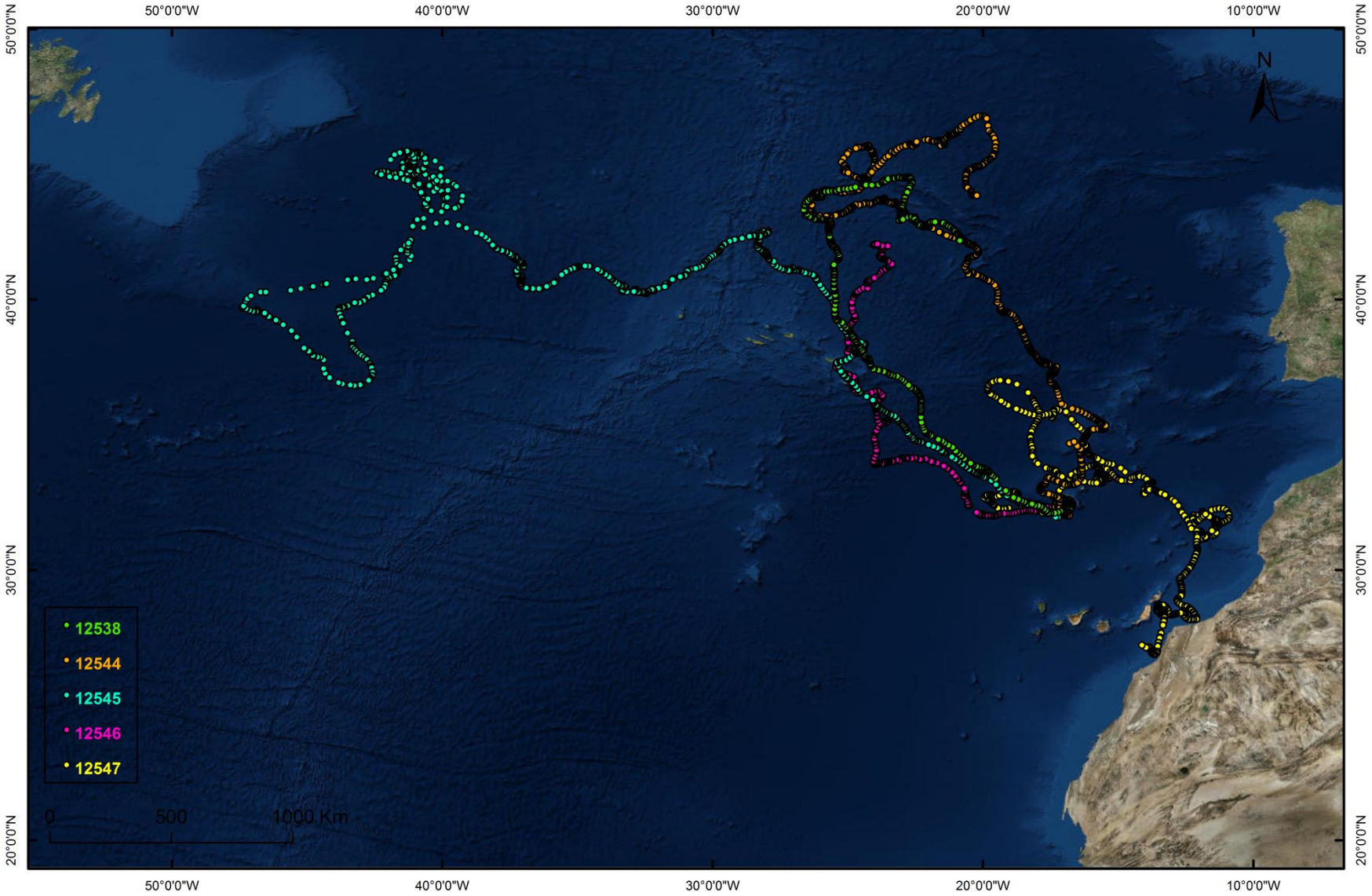


FIGURE 3 – Spring-tagged turtles' movements plotted over Google Earth Basemap (available in ArcMap™ (ESRI 2011))

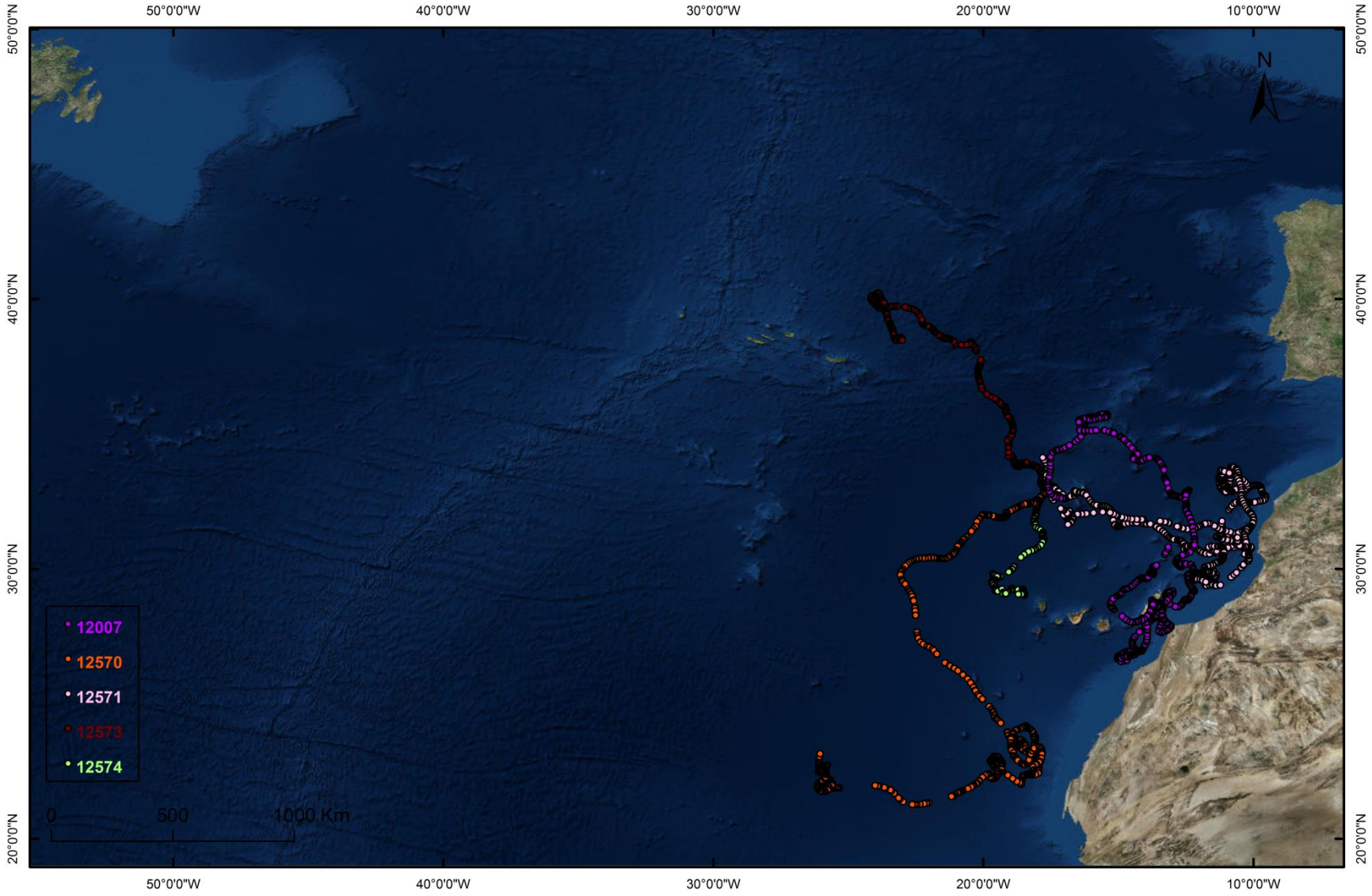


FIGURE 4 – Autumn-tagged turtles' movements plotted over Google Earth Basemap (available in ArcMap™ (ESRI 2011))

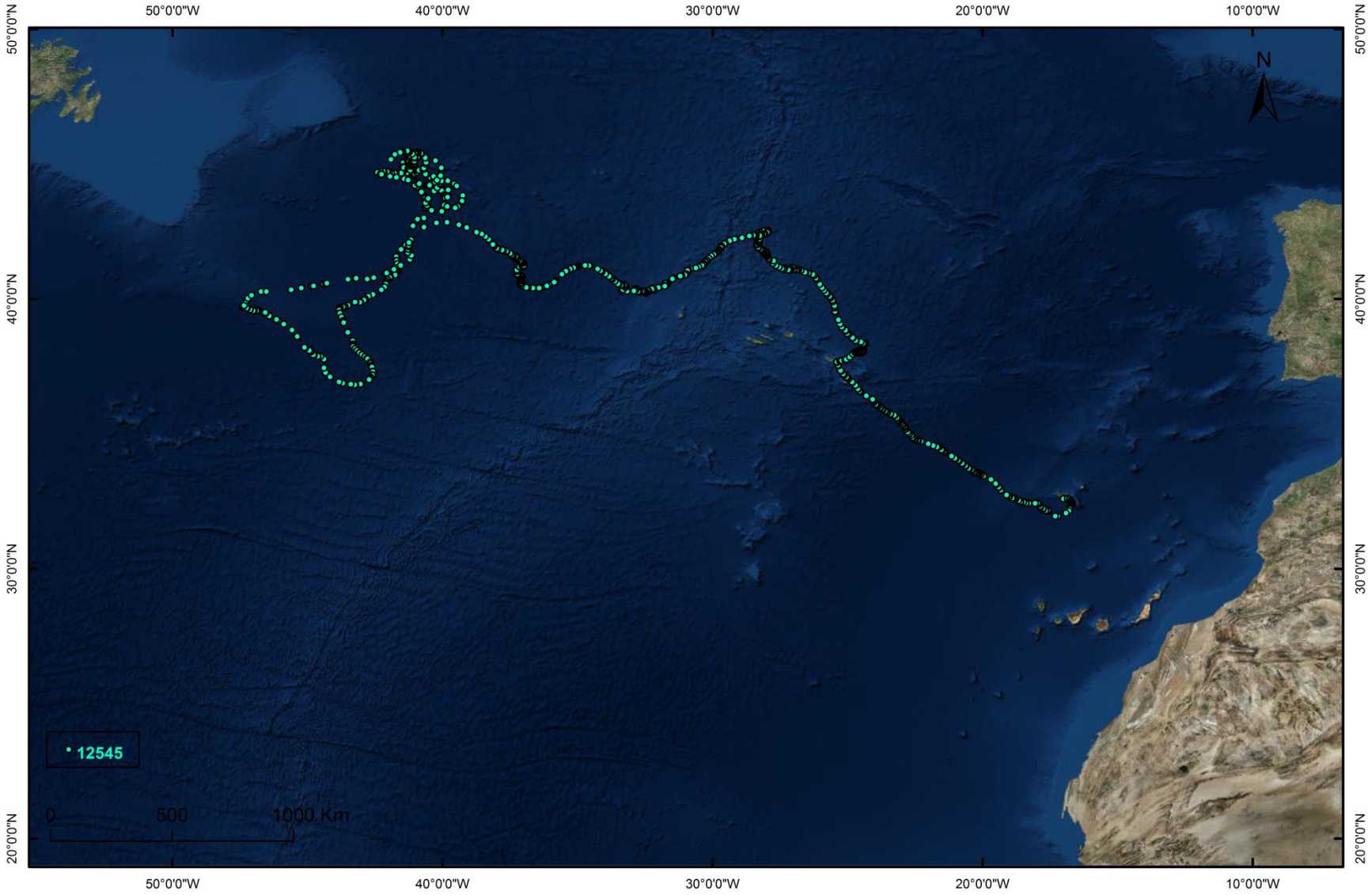


FIGURE 5 – Turtle ID 12545 movements plotted over Google Earth Basemap (available in ArcMap™ (ESRI 2011))

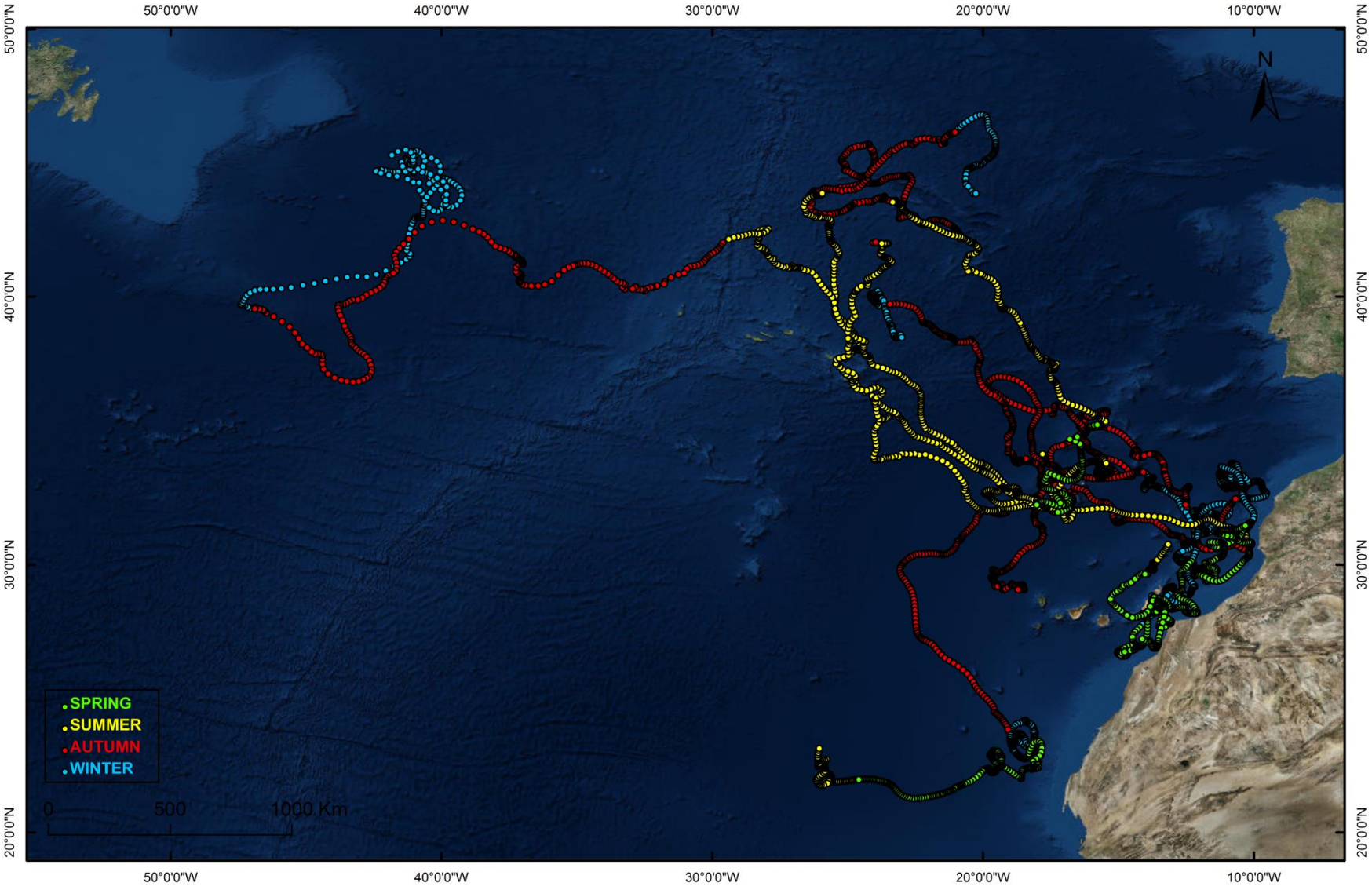


FIGURE 6 – Turtles' movements within seasons plotted over Google Earth Basemap (available in ArcMap™ (ESRI 2011))

B – ARS

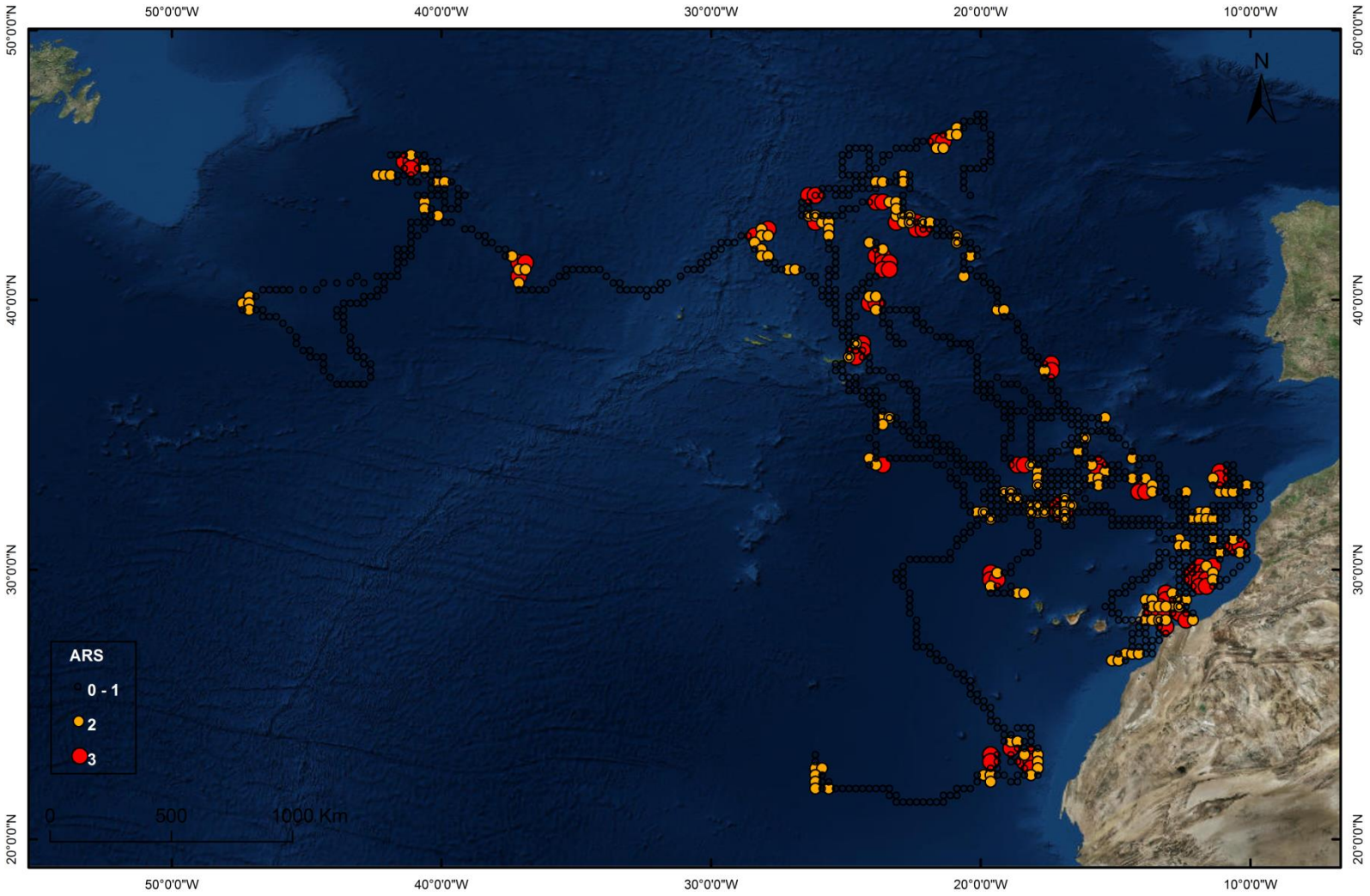


FIGURE 7 – ARS plotted over Google Earth Basemap (available in ArcMap™ (ESRI 2011)).

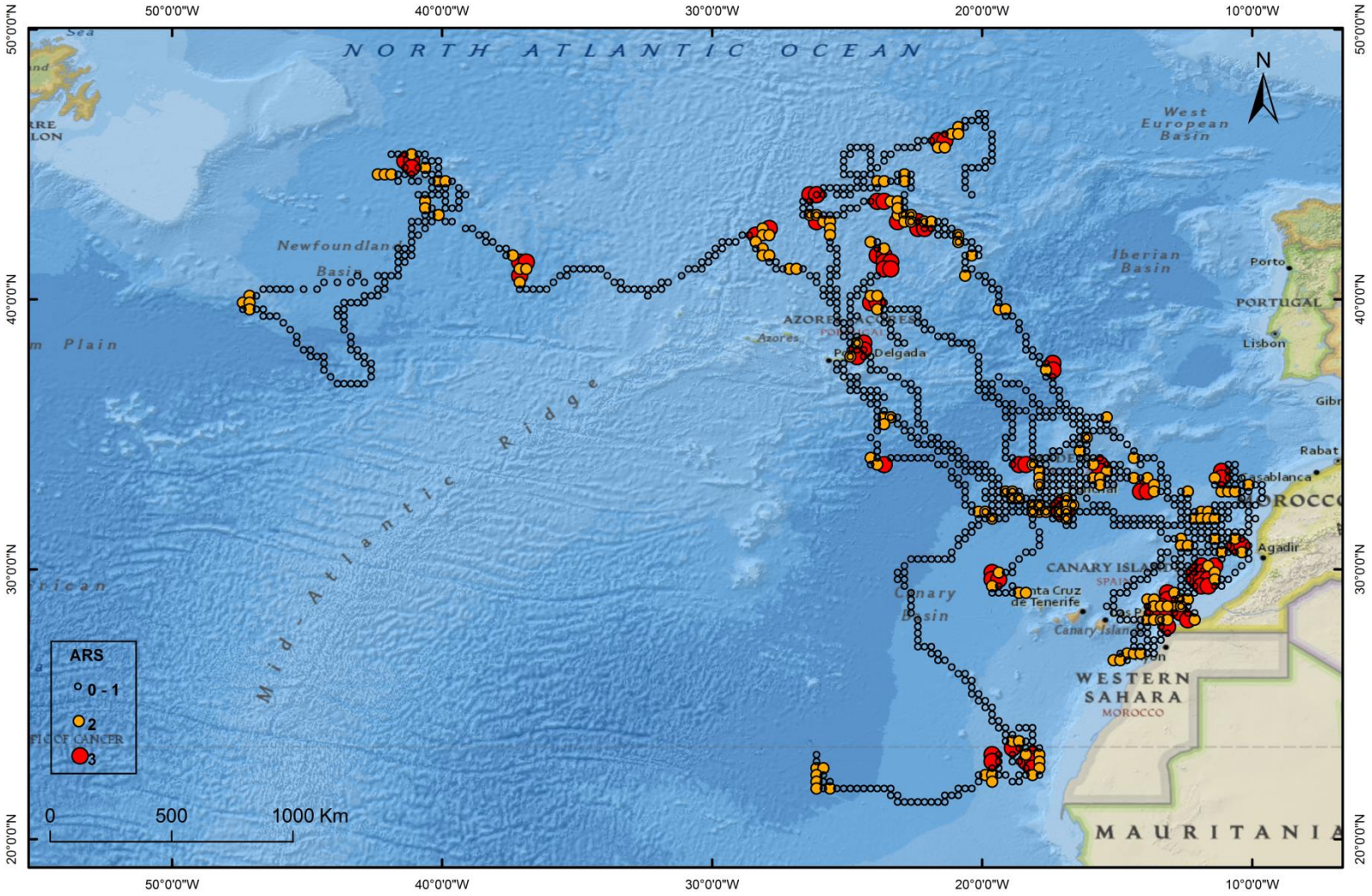


FIGURE 8 – ARS plotted over National Geographic Basemap (available in ArcMap™ (ESRI 2011)).

SPRING

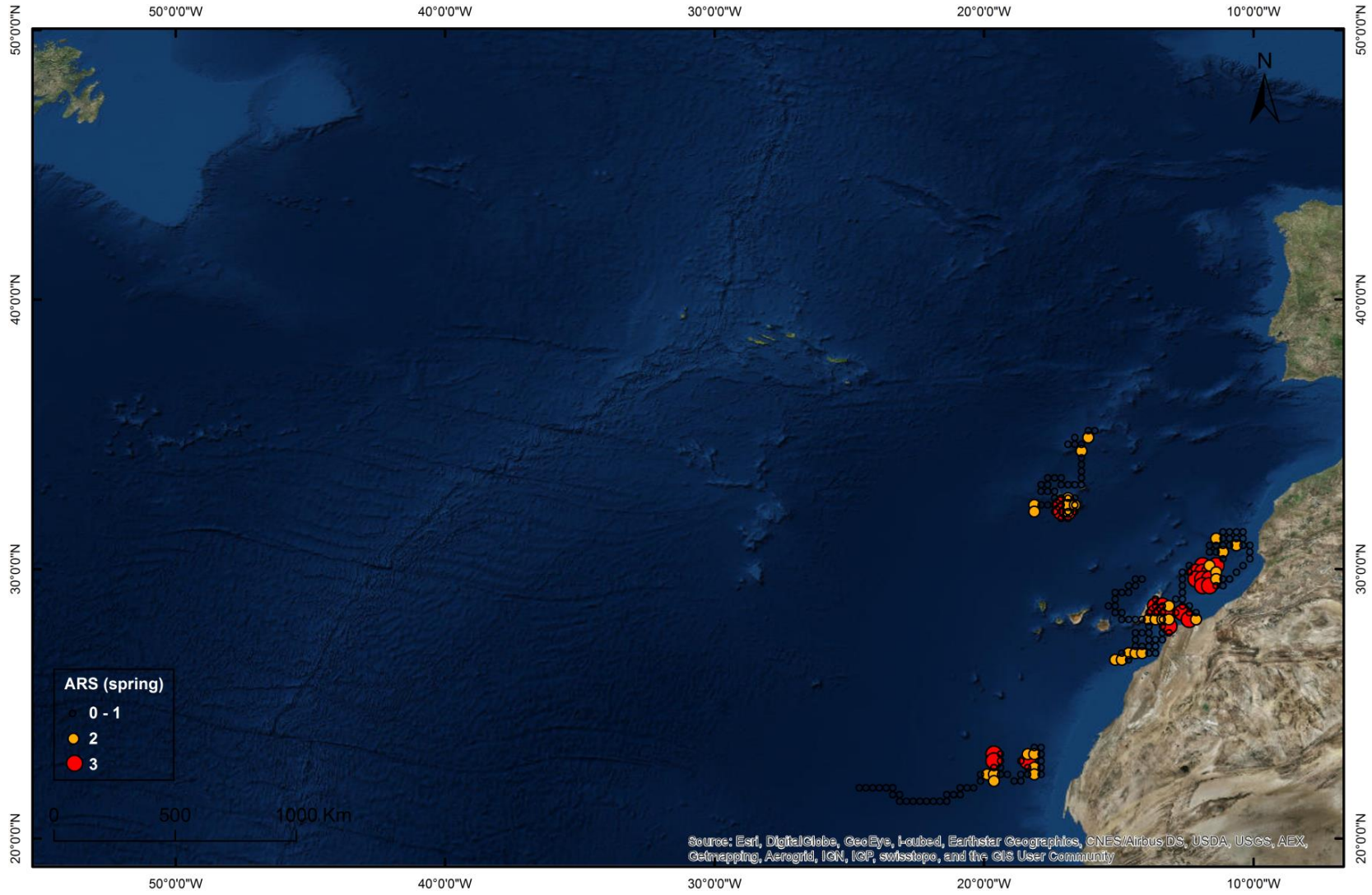


FIGURE 9 – Spring-ARS plotted over Google Earth Basemap (available in ArcMap™ (ESRI 2011)).

SUMMER

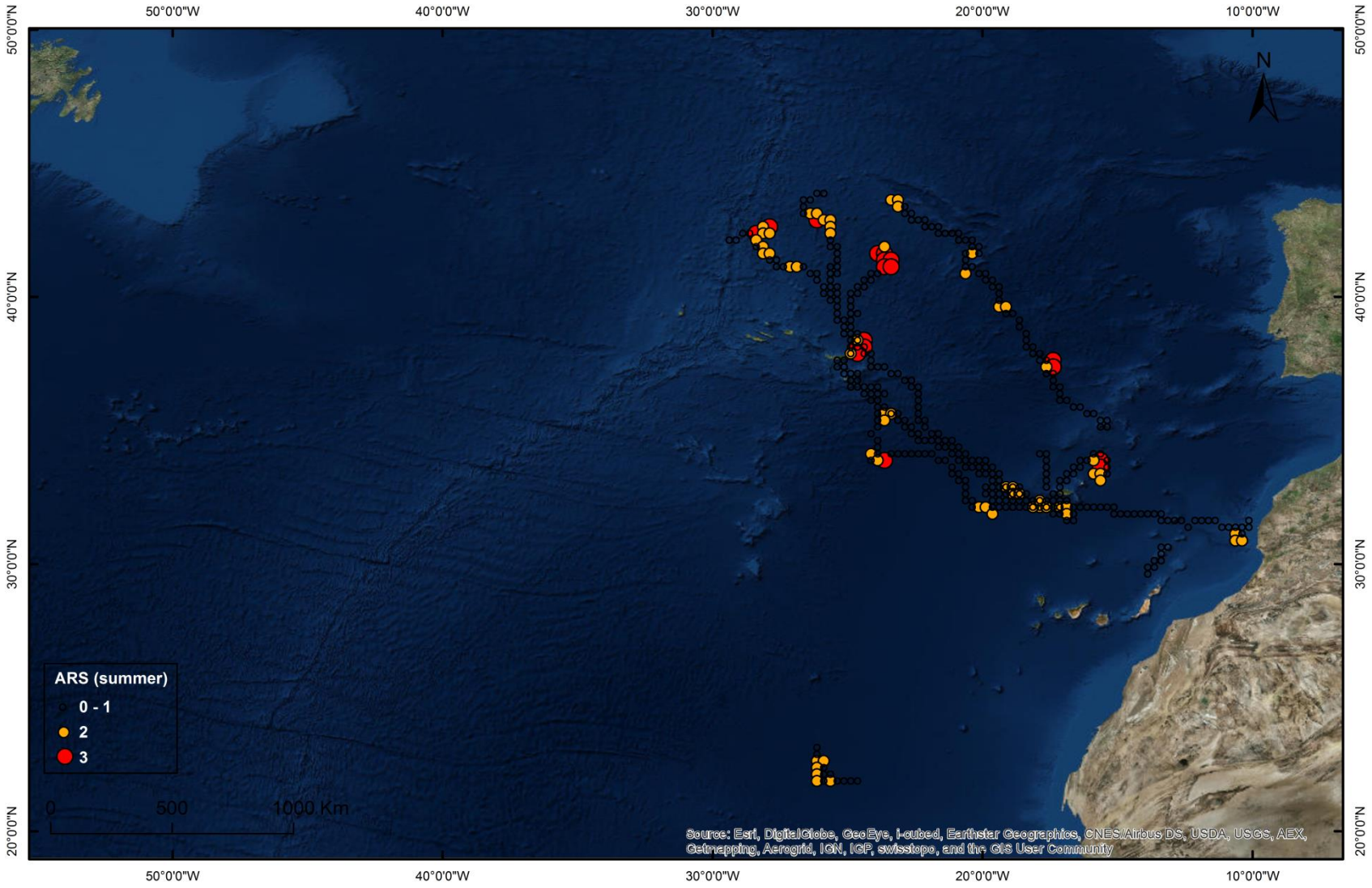


FIGURE 10 – Summer-ARS plotted over Google Earth Basemap (available in ArcMap™ (ESRI 2011)).

AUTUMN

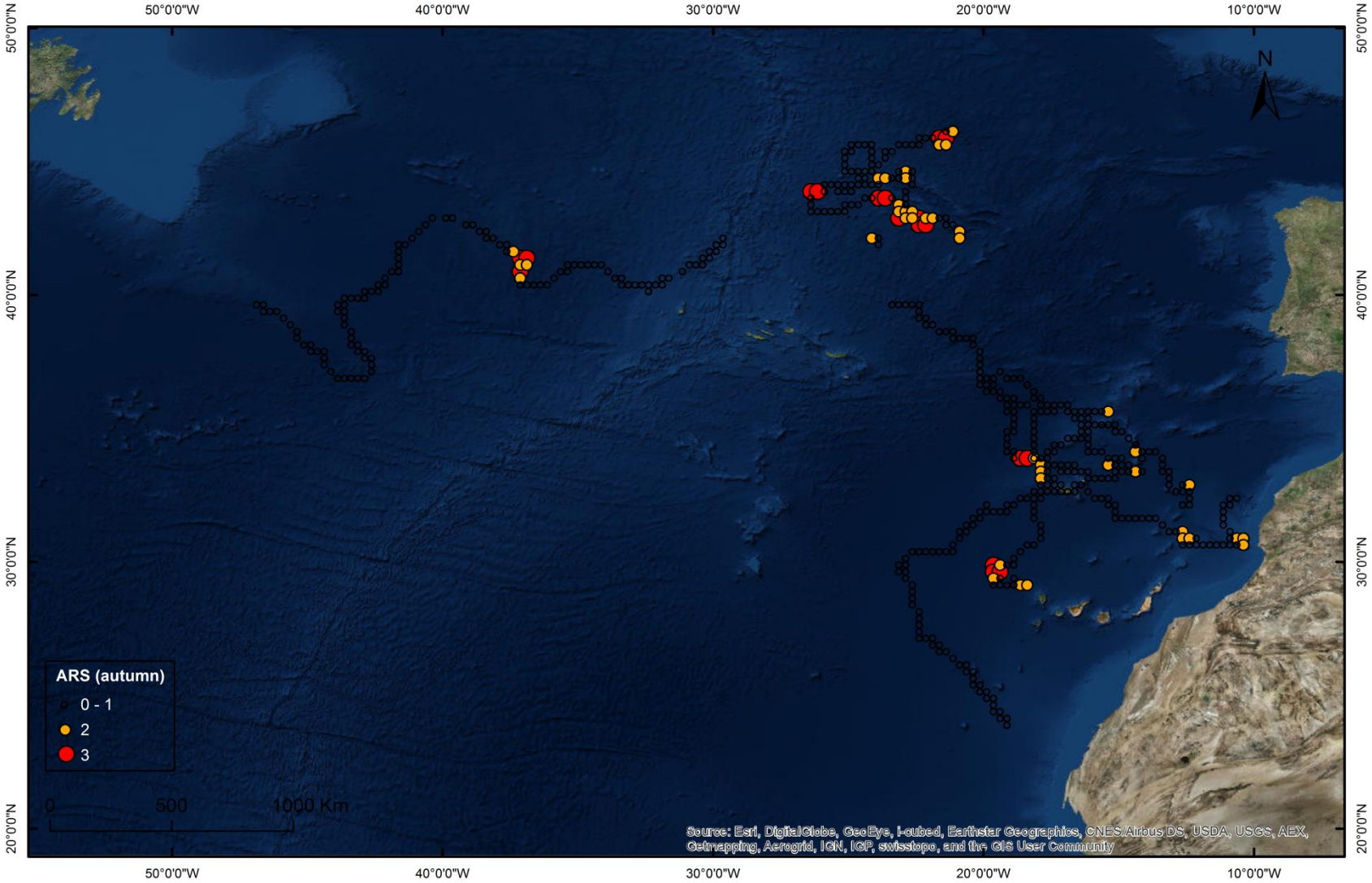


FIGURE 11 – Autumn-ARS plotted over Google Earth Basemap (available in ArcMap™ (ESRI 2011)).

WINTER

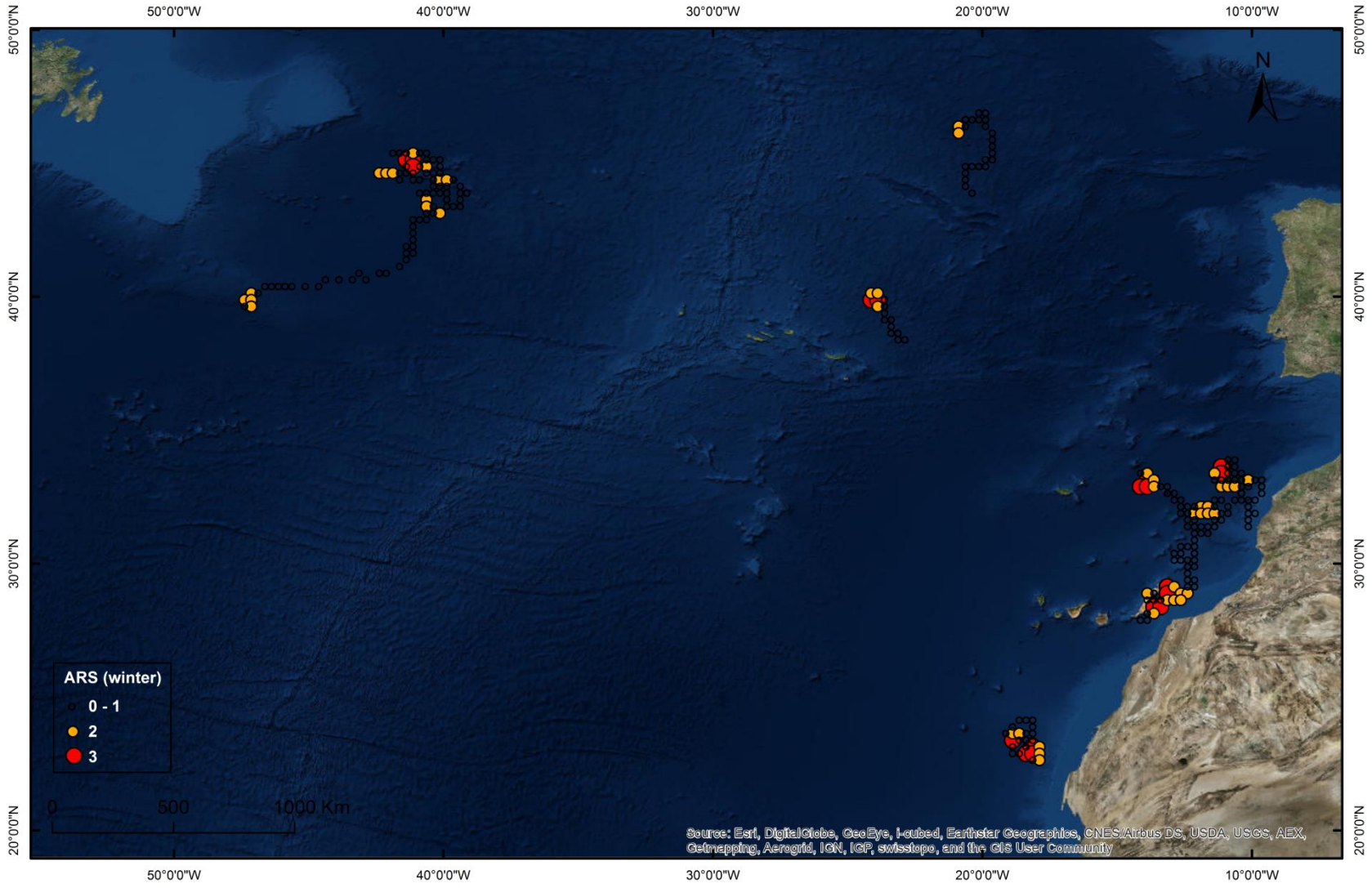


FIGURE 12 – Winter-ARS plotted over Google Earth Basemap (available in ArcMap™ (ESRI 2011)).

C – Environmental variables

BATHYMETRY

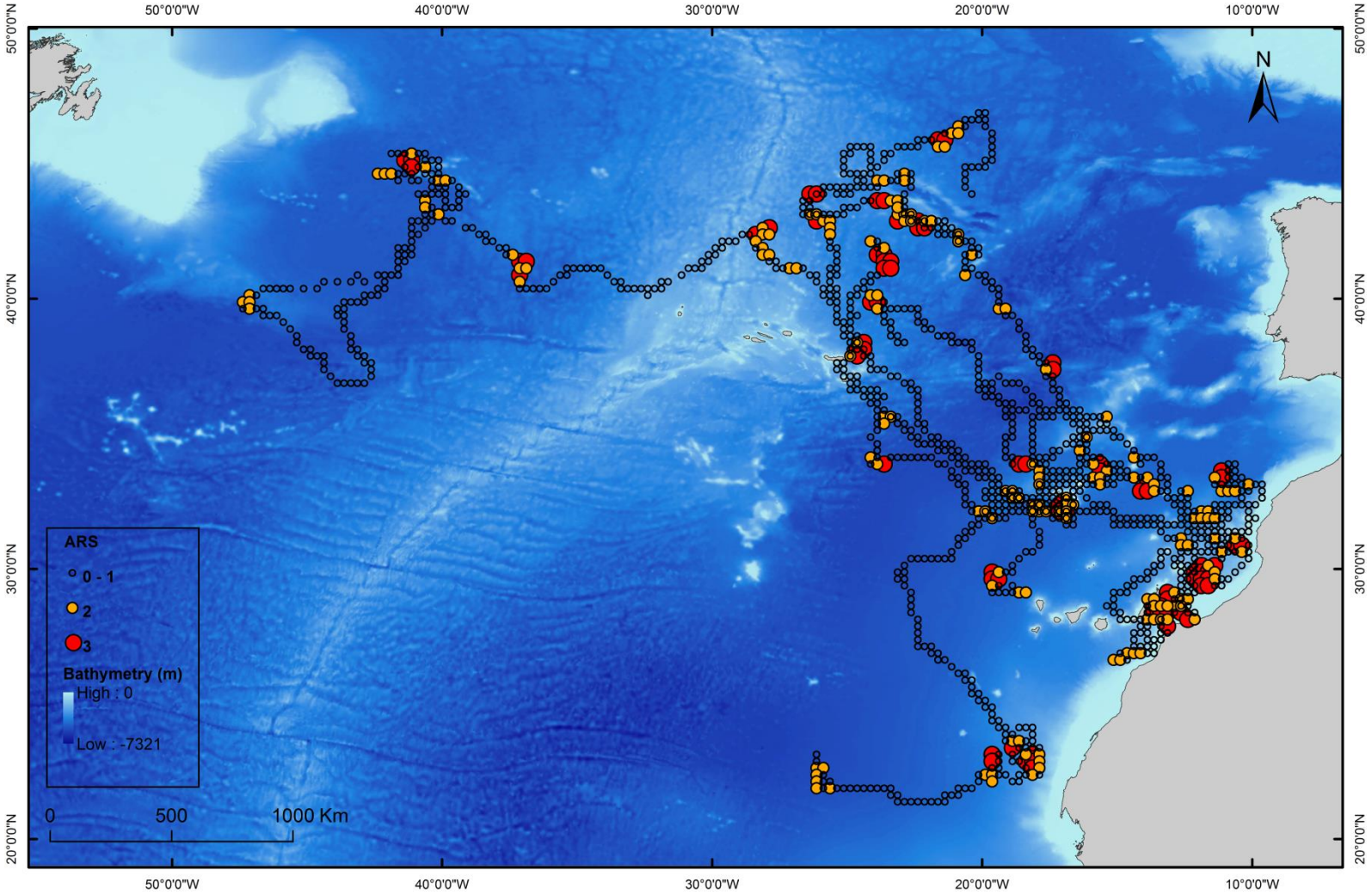


FIGURE 13 – ARS plotted over GEBCO bathymetry map

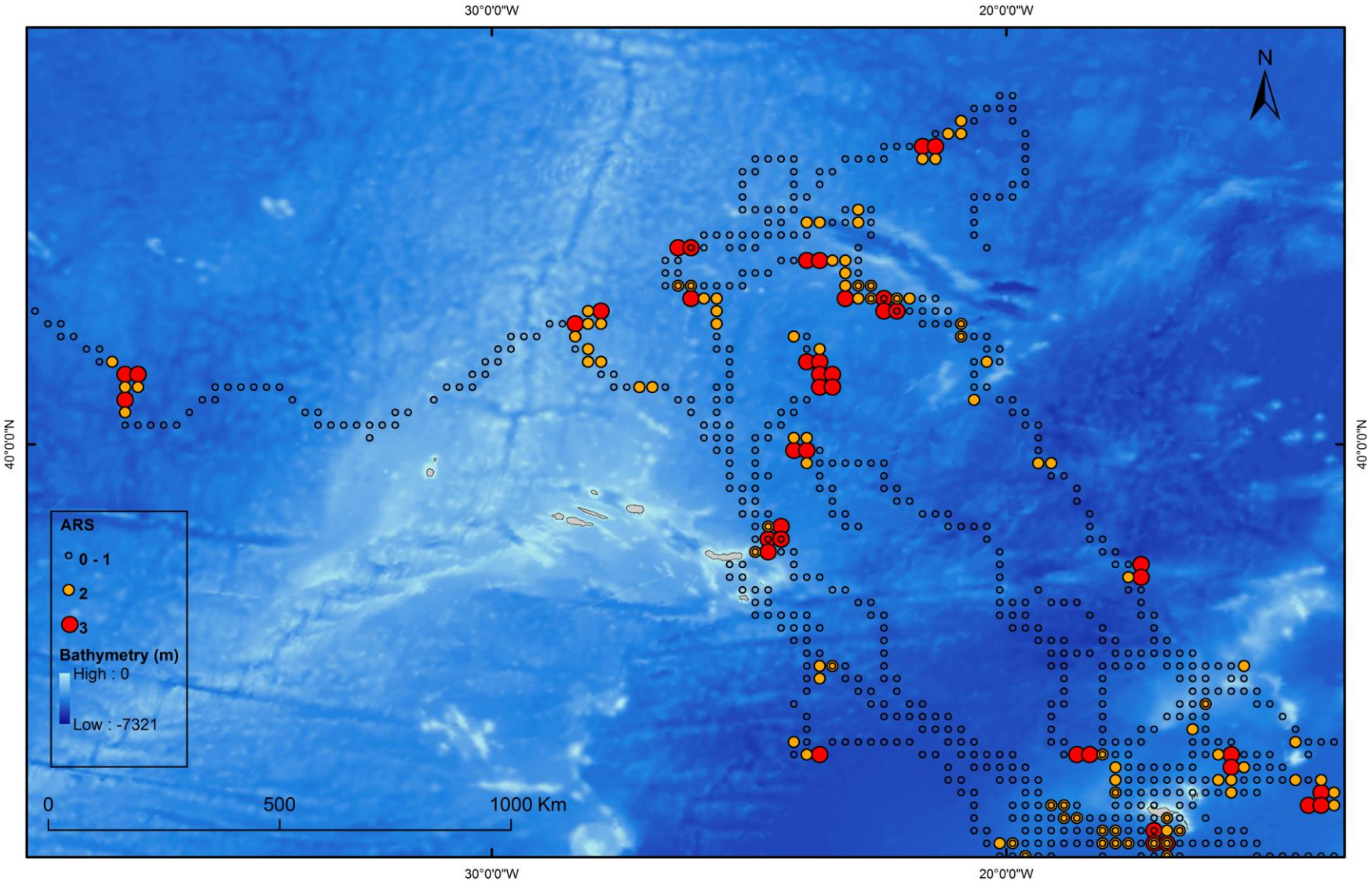


FIGURE 14 – ARS spring-tagged detail in a low bathymetry region located NE from Azores.

SST

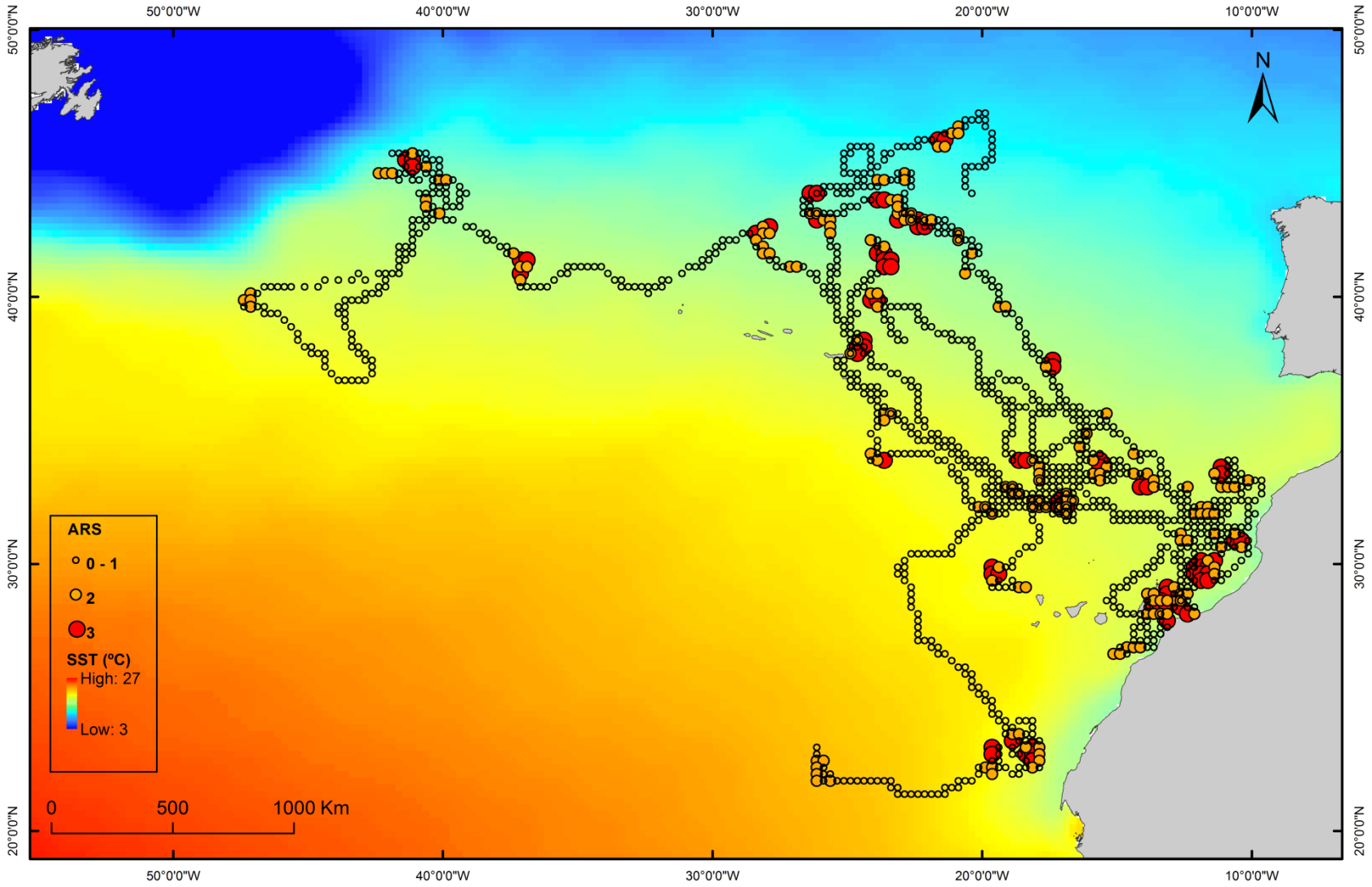


FIGURE 15 – ARS plotted over SST cumulative gridded map.

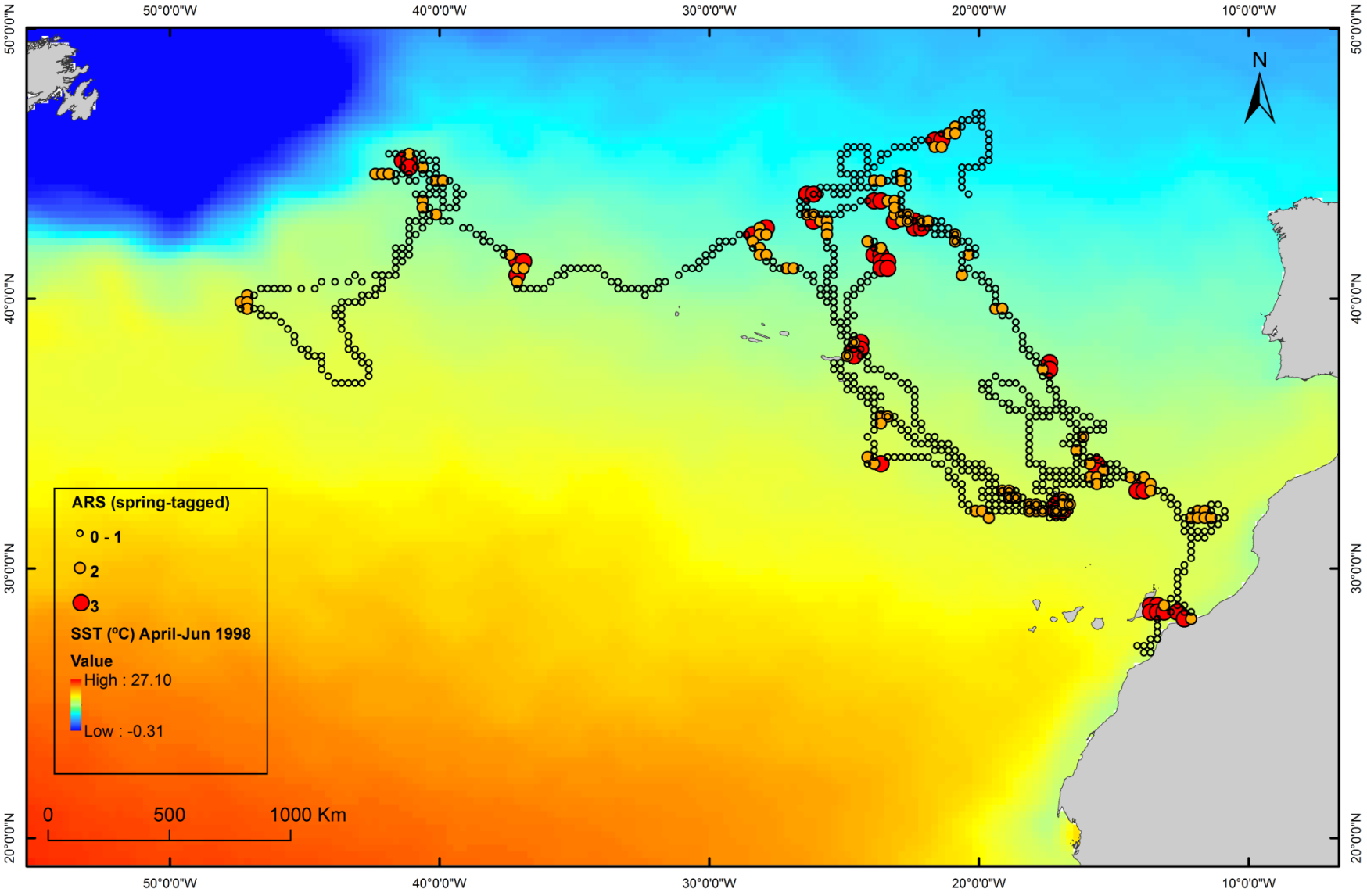


FIGURE 16 – Spring-tagged turtles ARS plotted over 3 months (April-Jun 1998) SST gridded map.

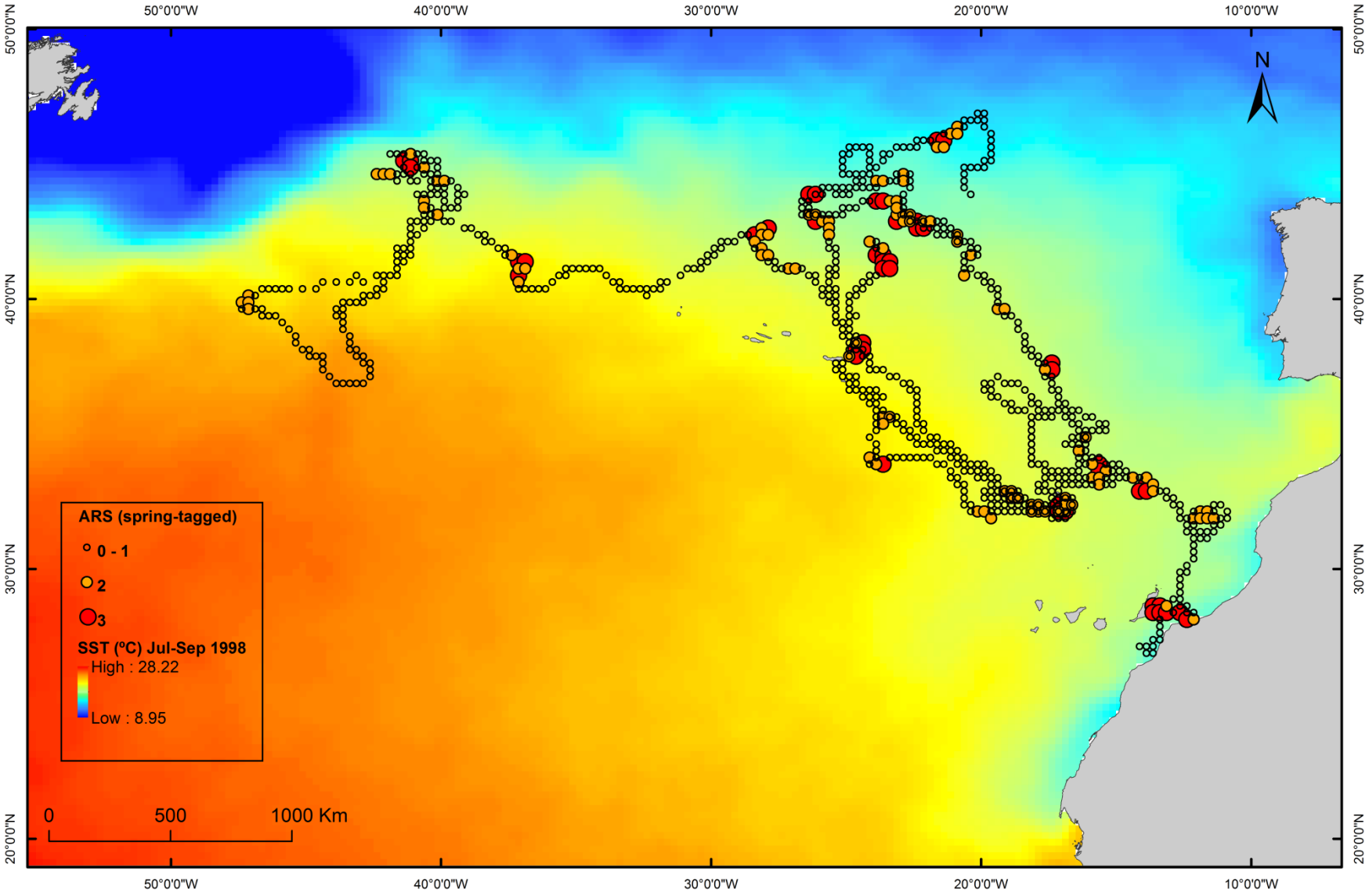


FIGURE 17 – Spring-tagged turtles ARS plotted over 3 months (Jul-Sep 1998) SST gridded map.

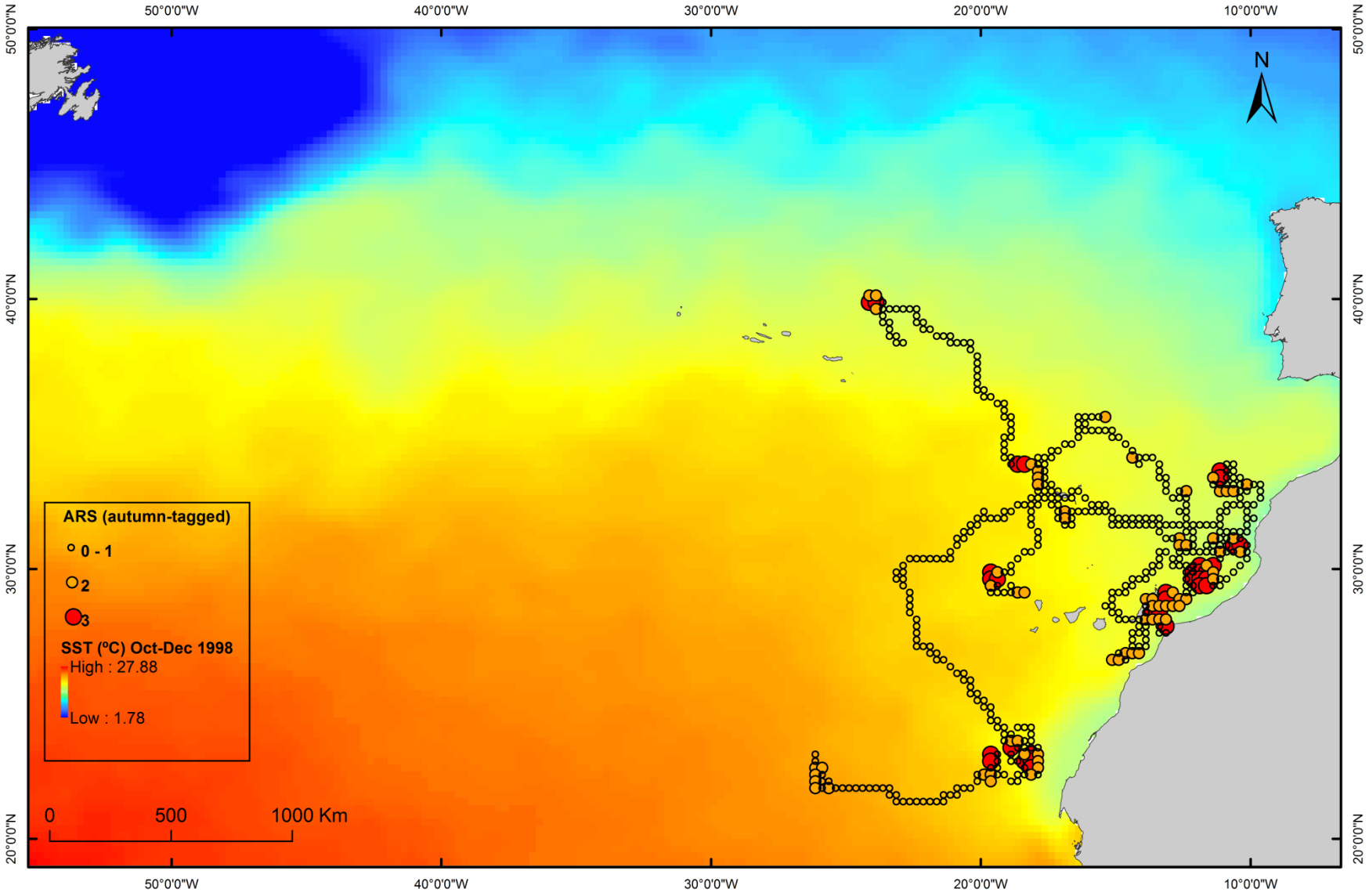


FIGURE 18 – Autumn-tagged turtles ARS plotted over 3 months (Oct-Dec 1998) SST gridded map.

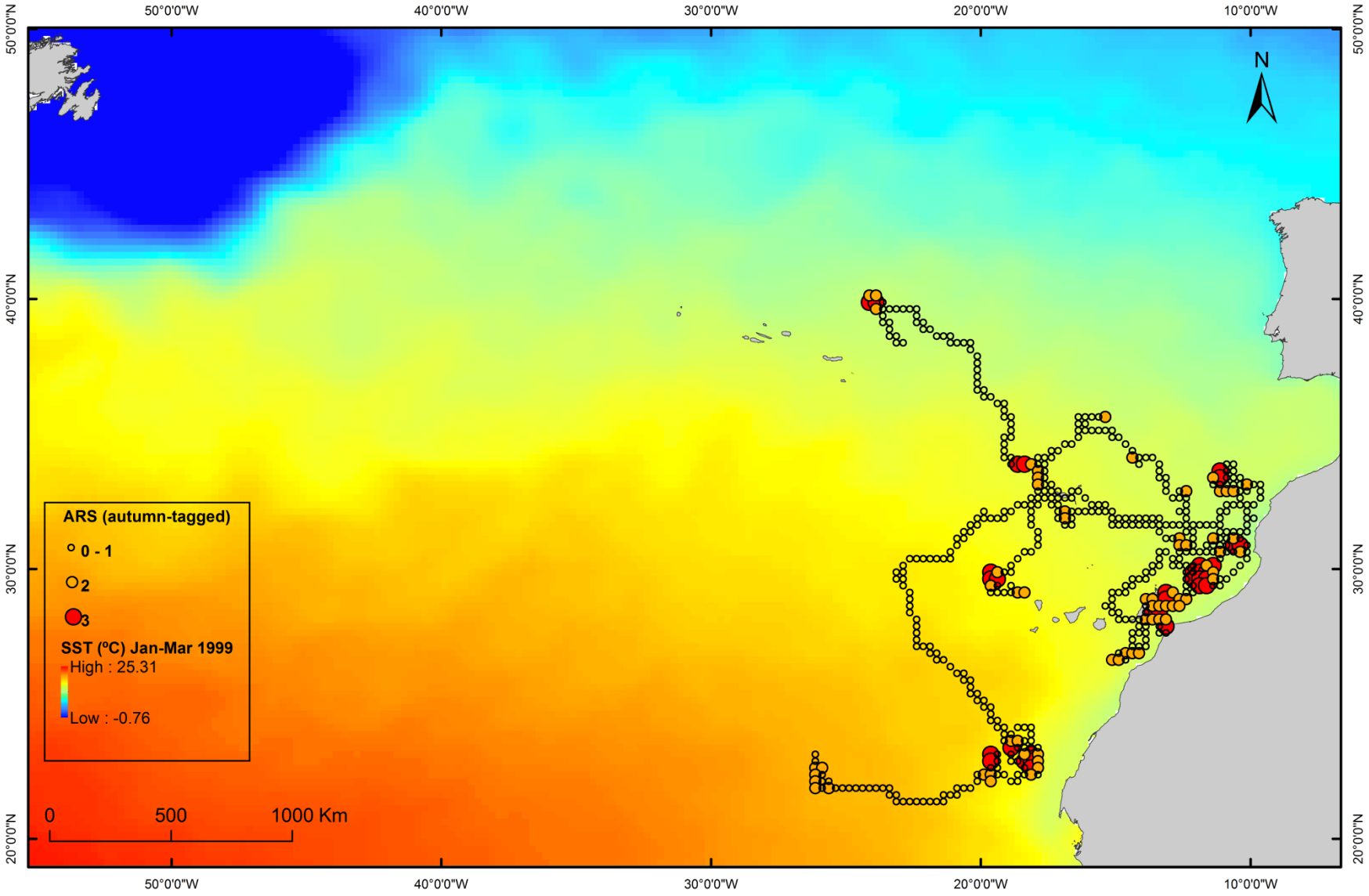


FIGURE 19 – Autumn-tagged turtles ARS plotted over 3 months (Jan-Mar 1999) SST gridded map.

SSH

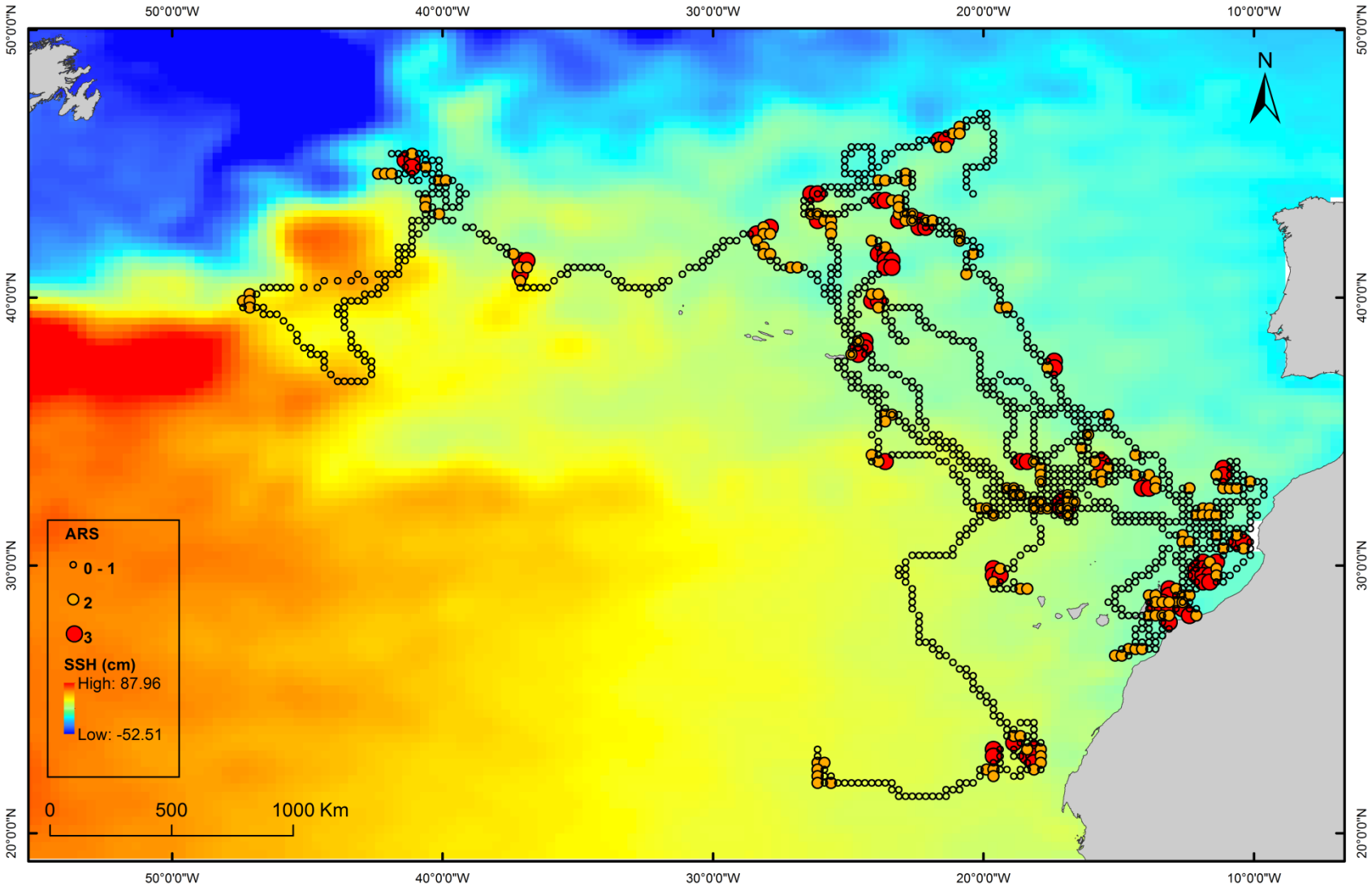


FIGURE 20 – ARS plotted over cumulative SSH gridded map.

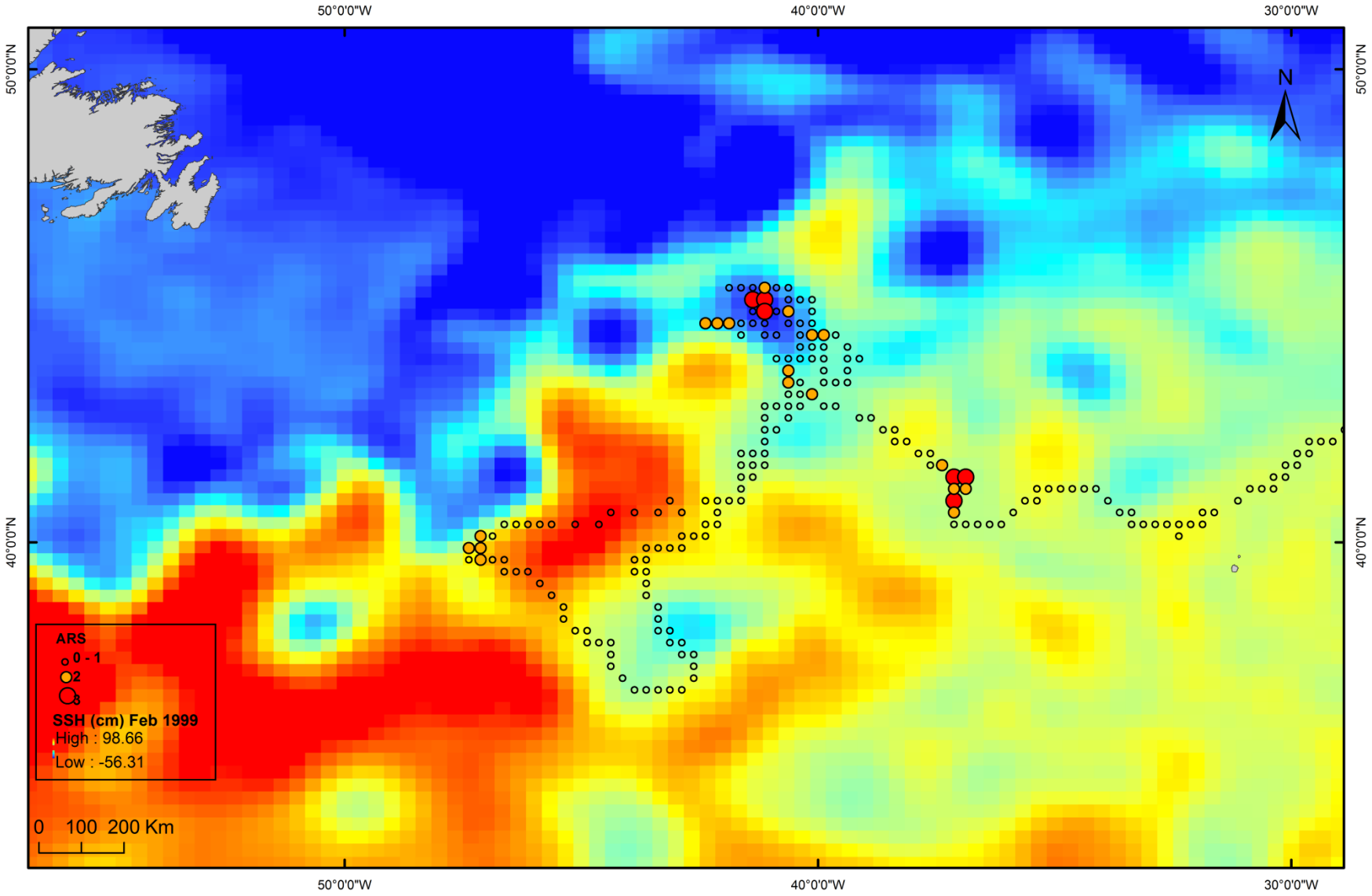


FIGURE 21 – ID 12545 ARS detail plotted over monthly (February 1999) SSH gridded map.

SSHA

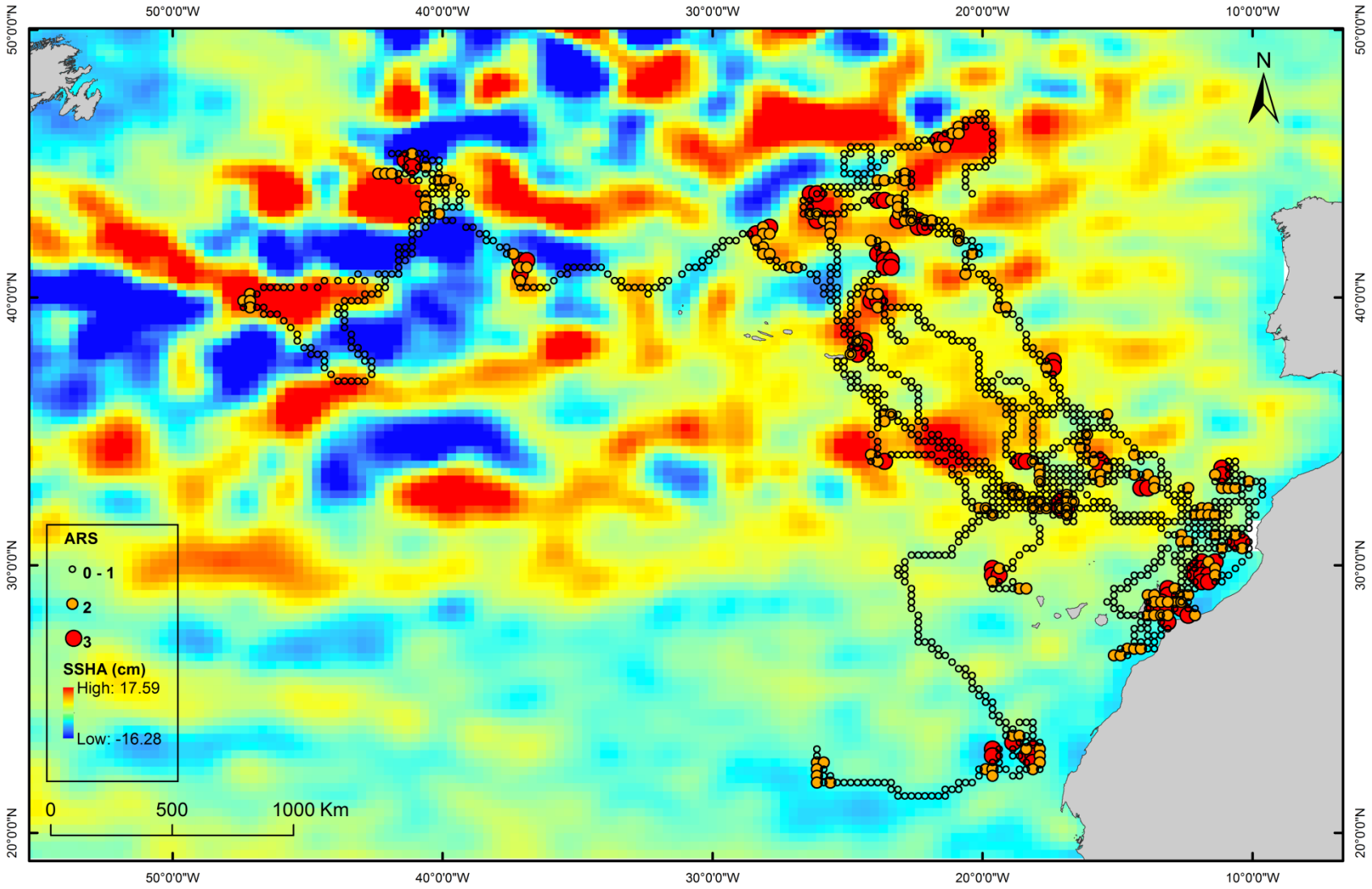


FIGURE 22 – ARS plotted over cumulative SSHA gridded map.

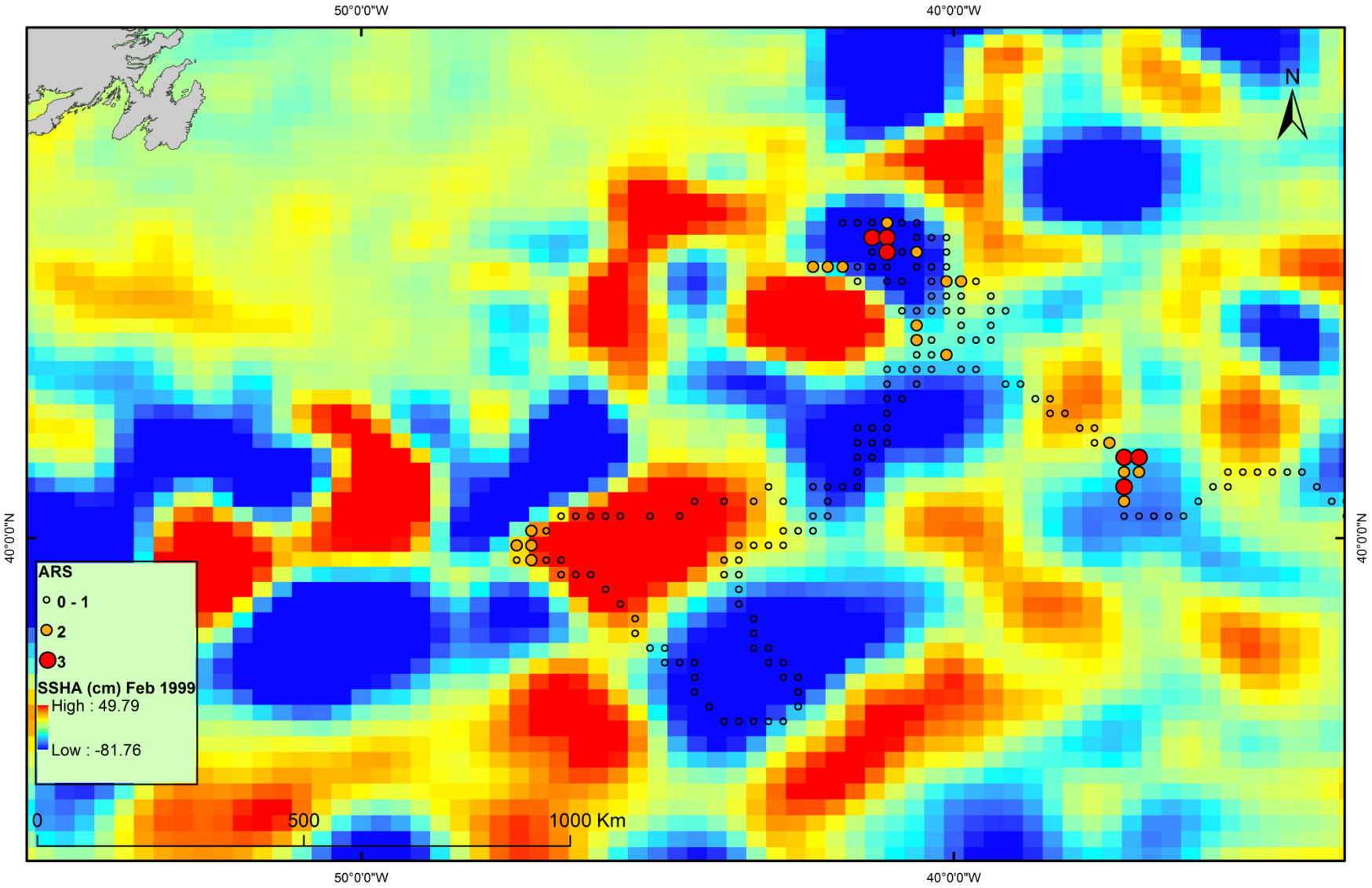


FIGURE 23 – ID 12545 ARS detail plotted over monthly (Febuary) SSHA gridded map.

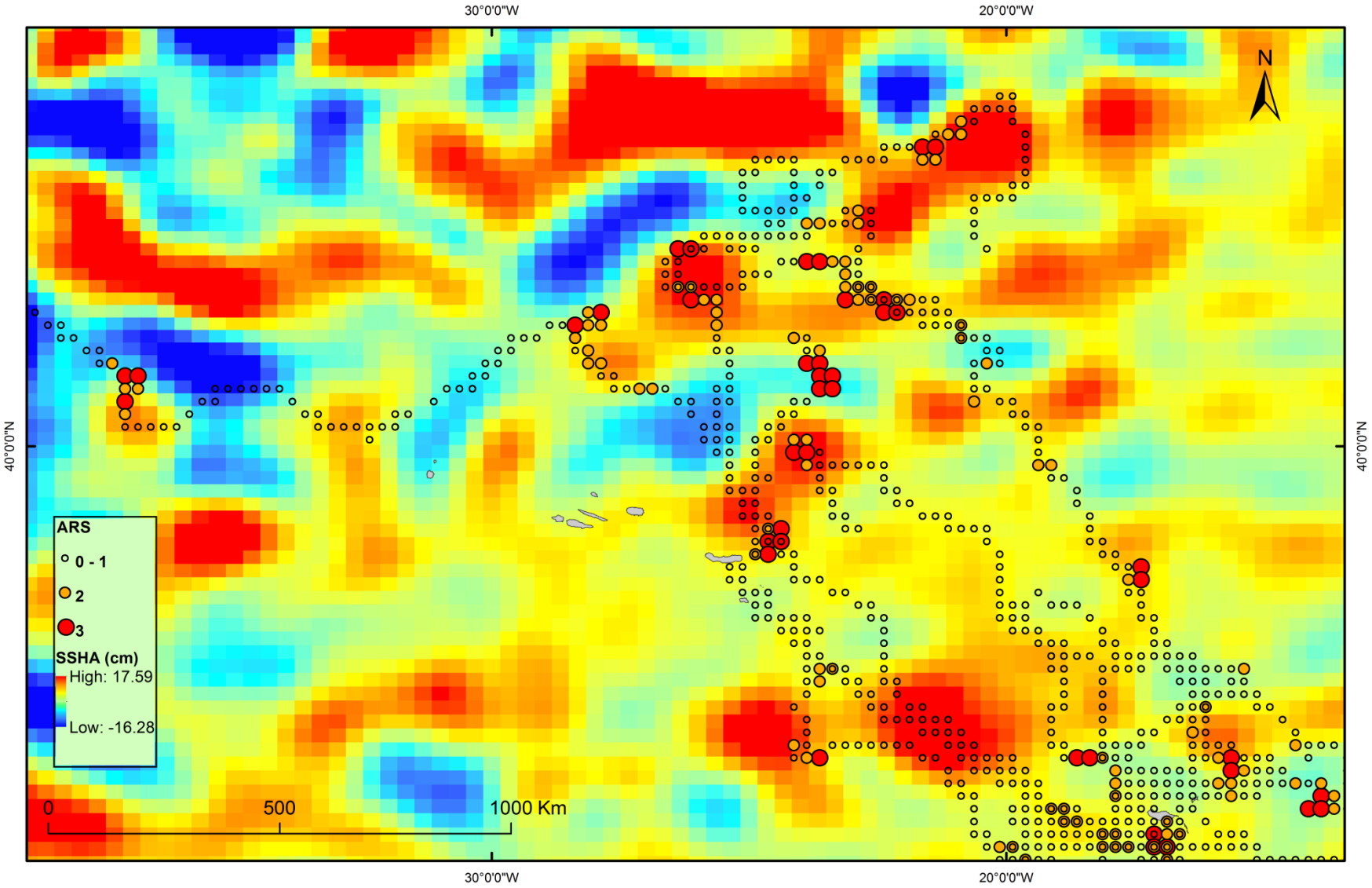


FIGURE 24 – Spring-tagged ARS detail plotted over cumulative SSHA gridded map.

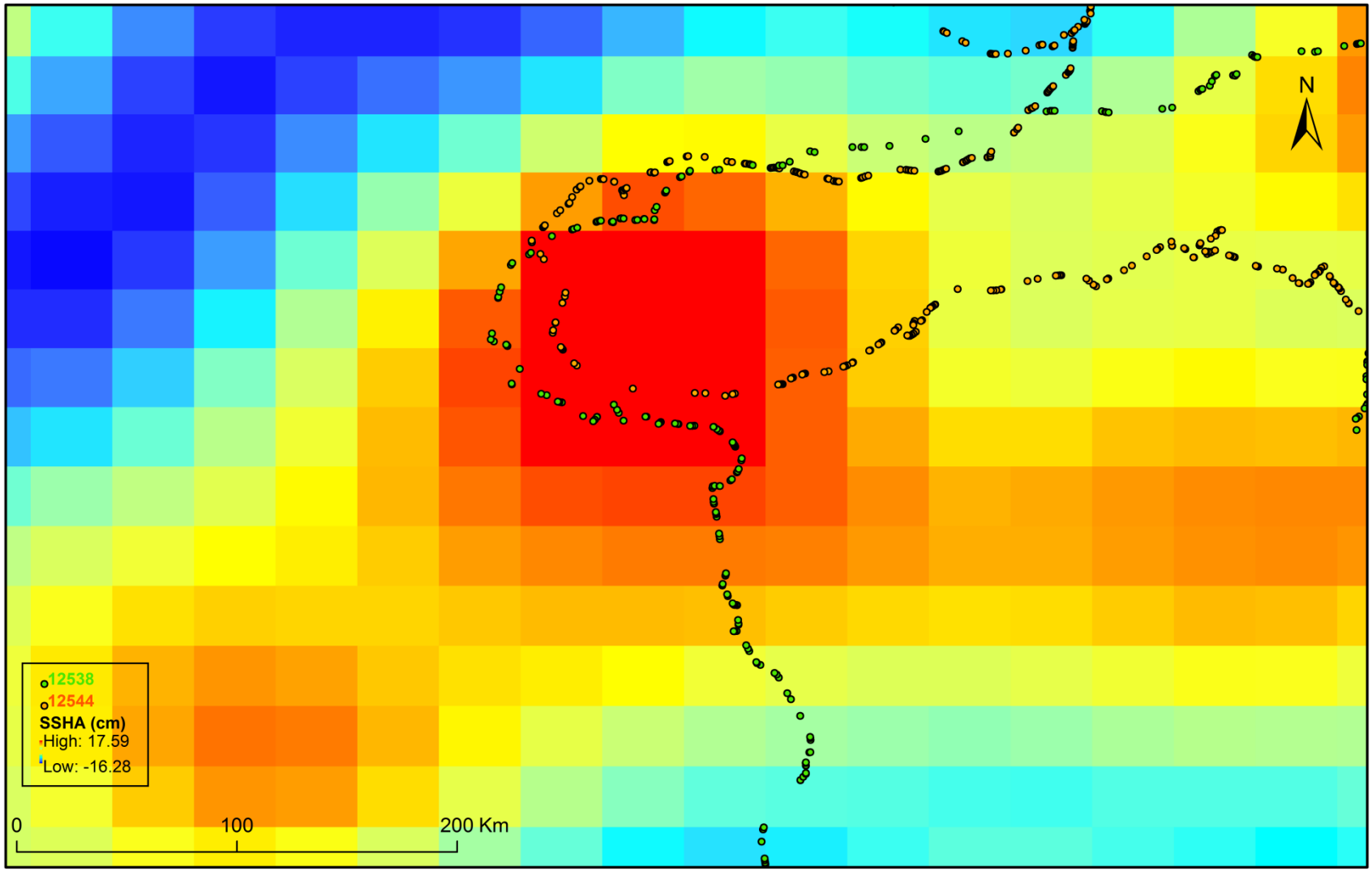


FIGURE 25 – Spring-tagged turtles IDs 12538 and 12544 movement detail plotted over cumulative SSHA gridded map.

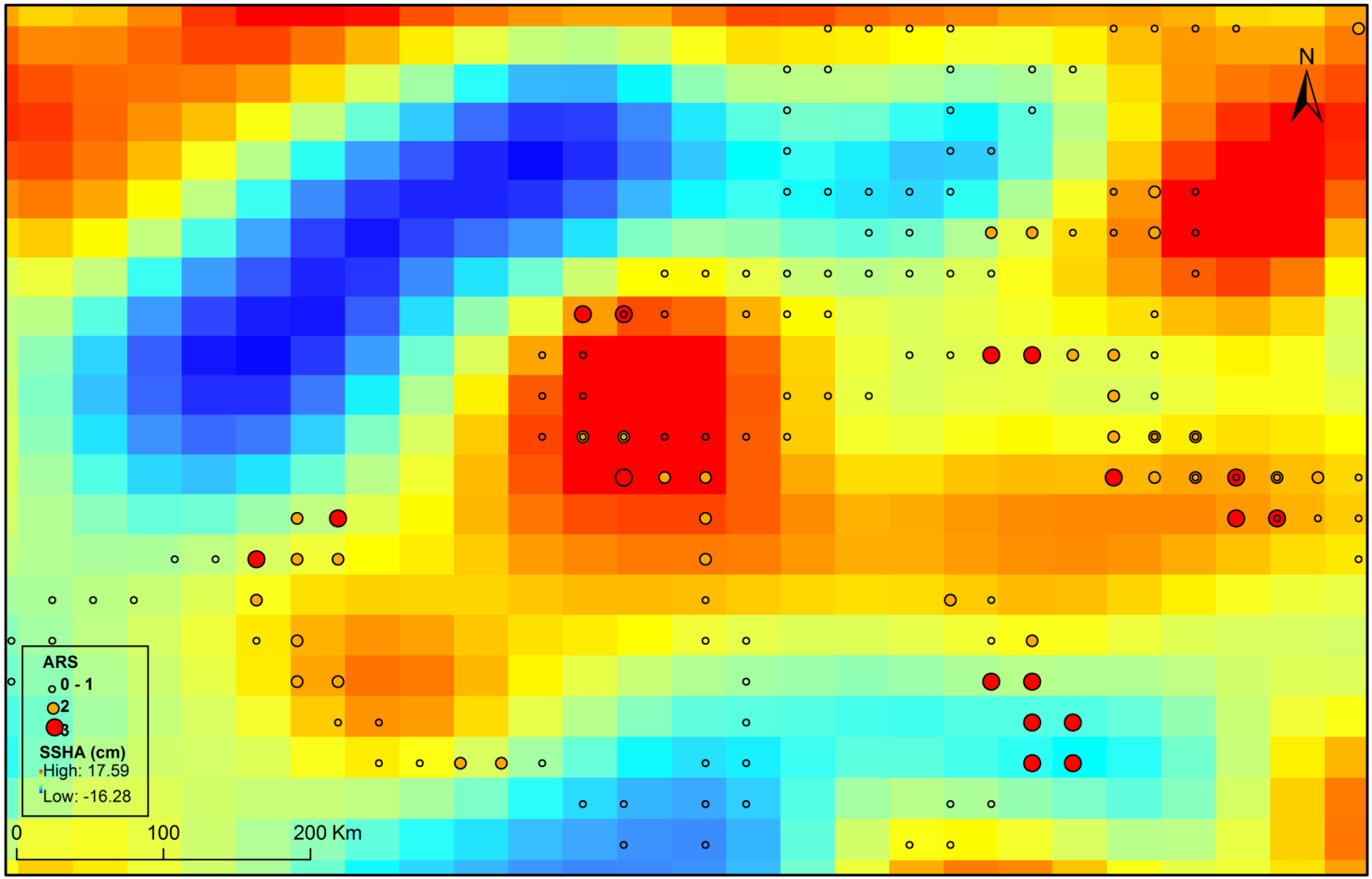


FIGURE 26 – Spring-tagged turtles IDs 12538 and 12544 ARS detail plotted over cumulative SSHA gridded map.

CHLA

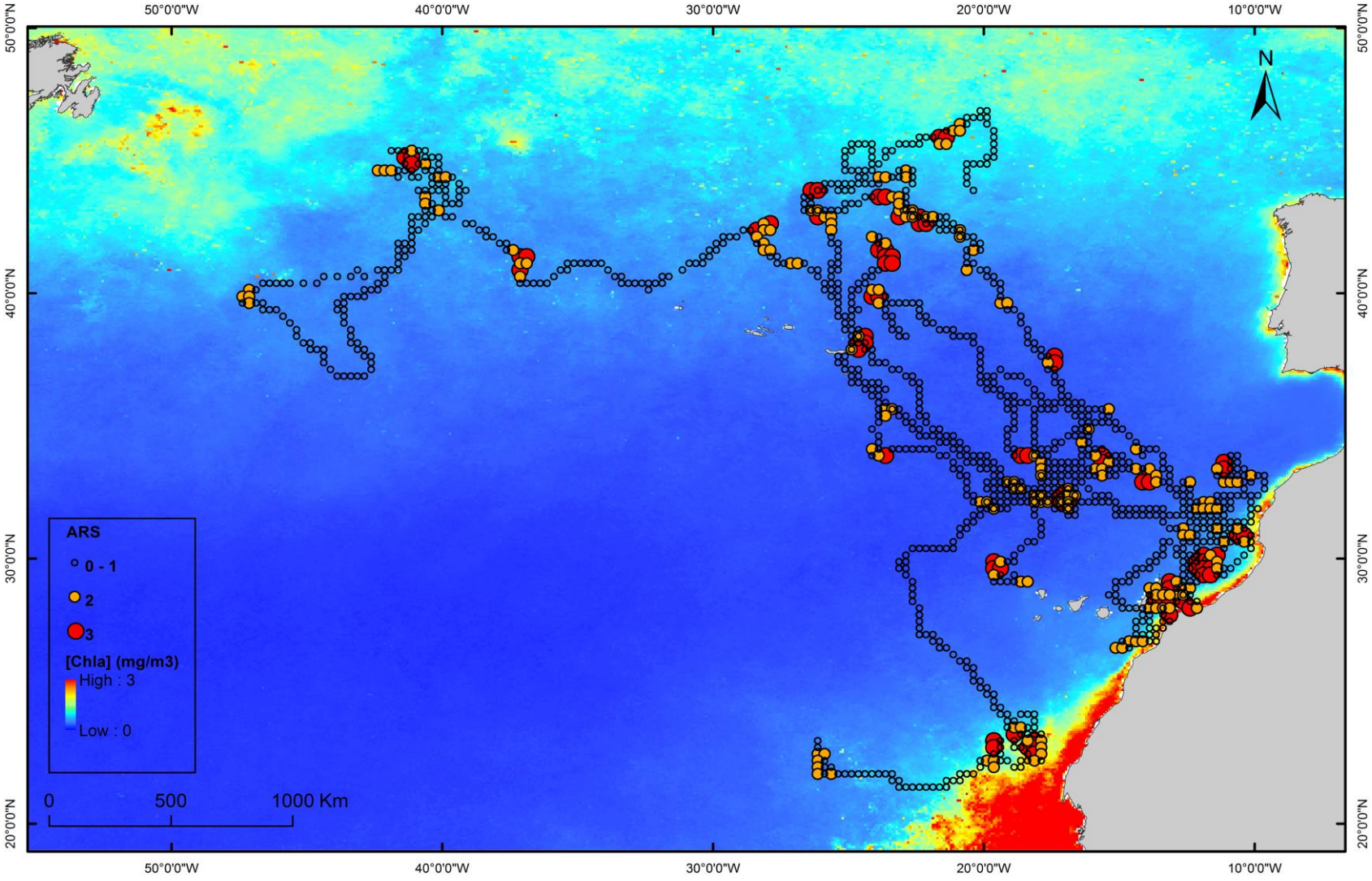


FIGURE 27 – ARS plotted over cumulative Chl*a* gridded map.

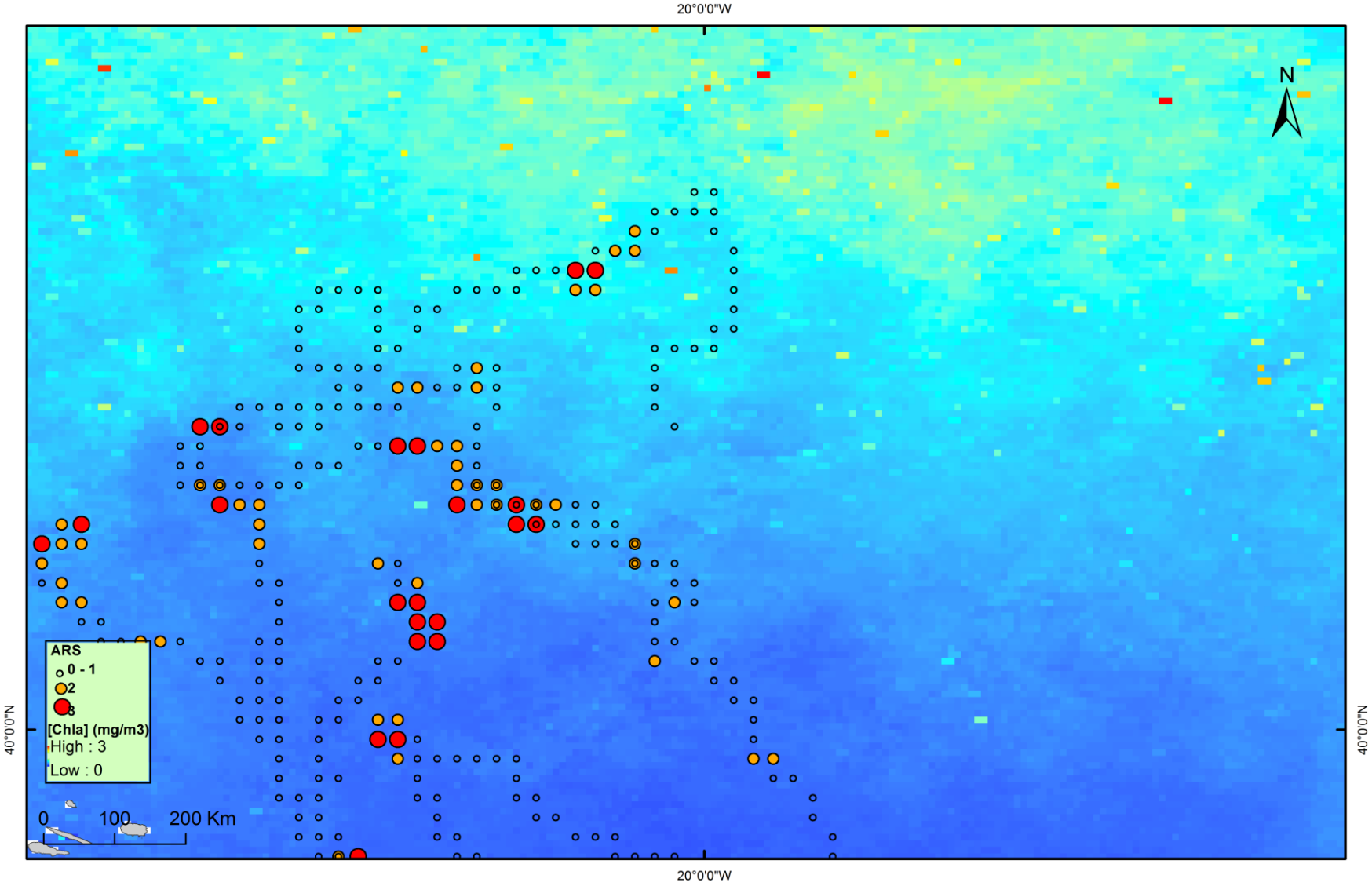


FIGURE 28 – ID 12538 and ID 12544 ARS detail plotted over cumulative Chl*a* gridded map.

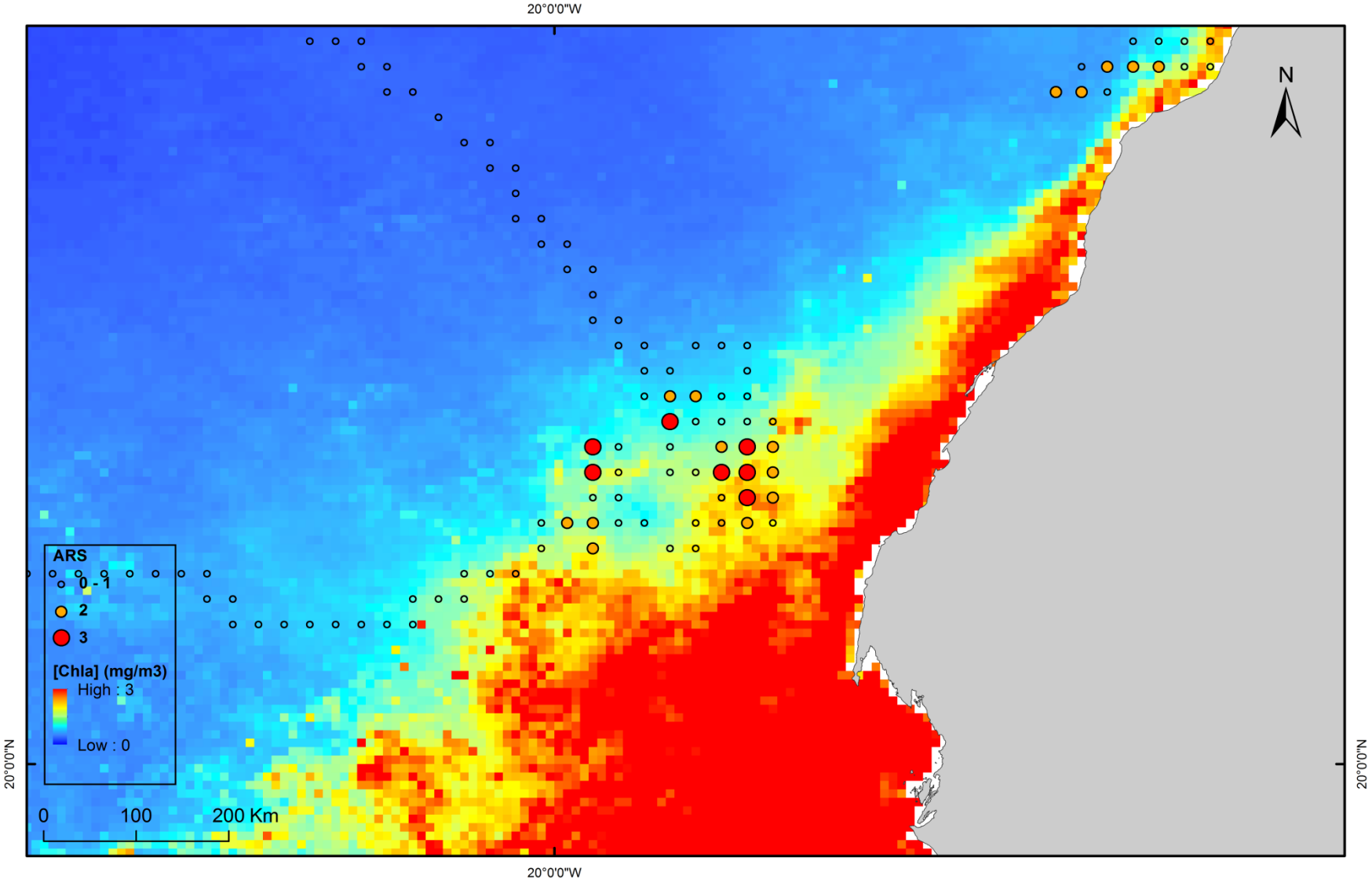


FIGURE 29 – ID 12570 ARS detail plotted over cumulative Chl*a* gridded map.

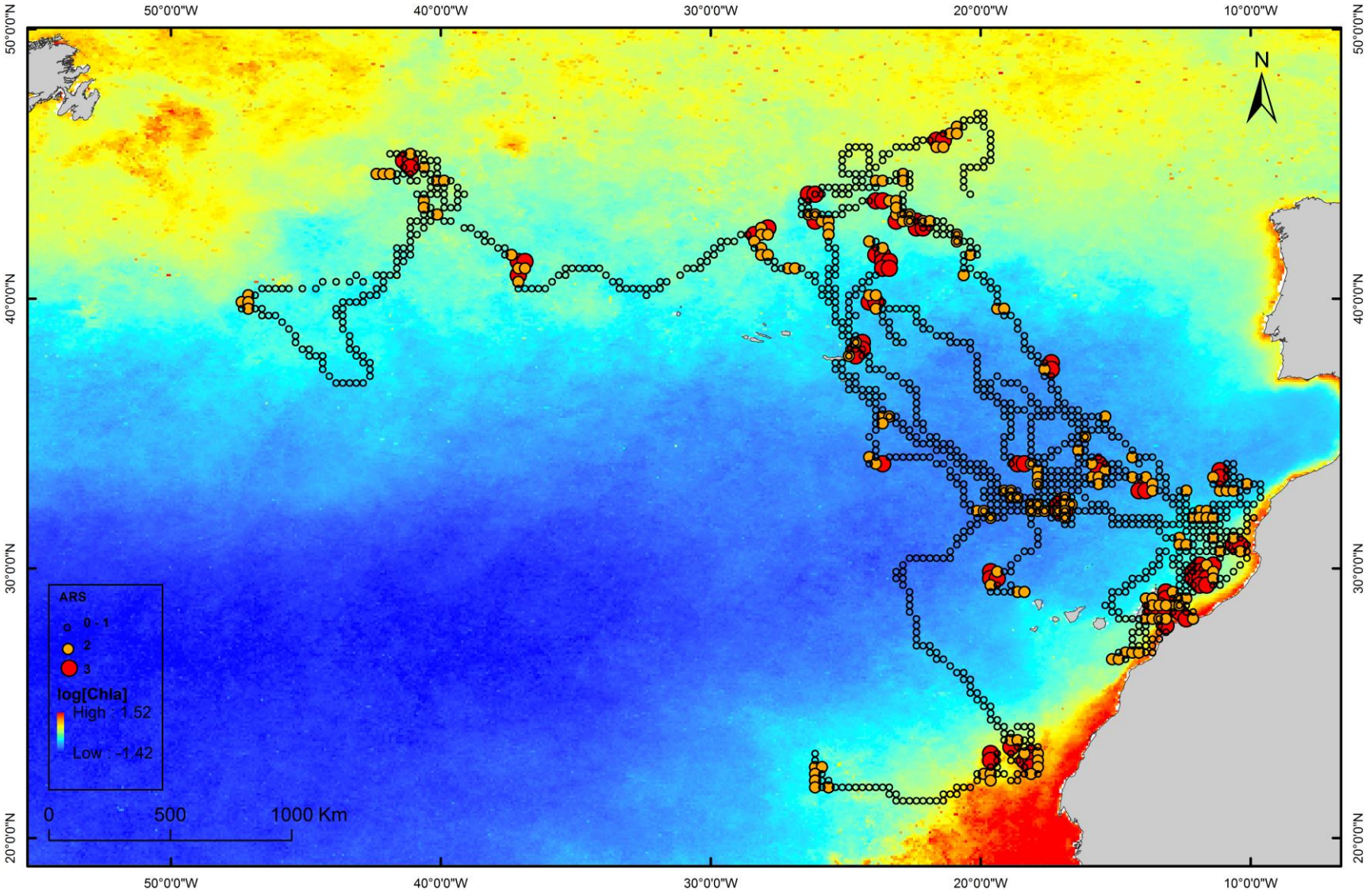
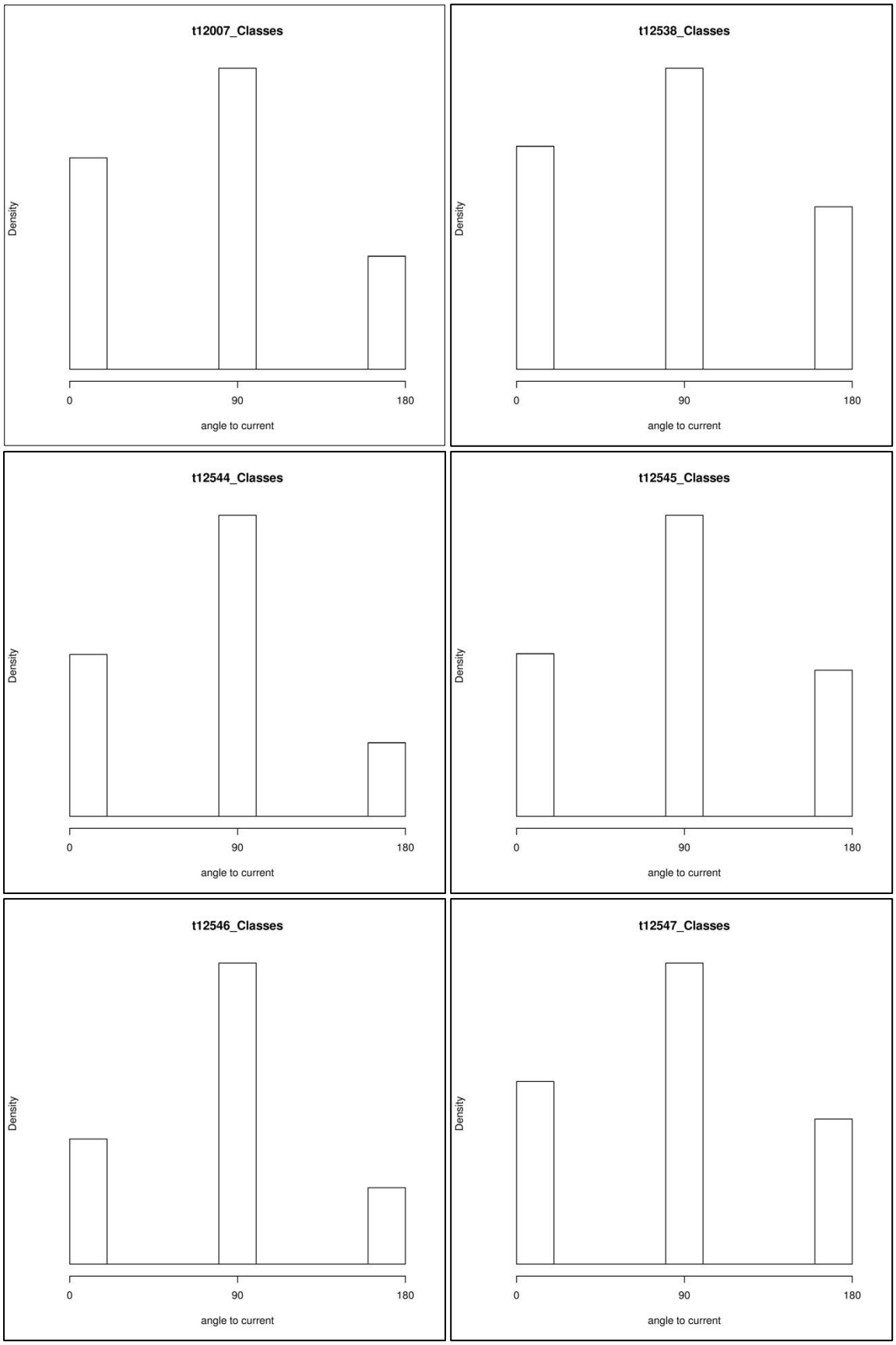


FIGURE 30 – ARS plotted over cumulative log-transformed Chl*a* gridded map.

APPENDIX II – Turtles' angles in relation to ocean currents



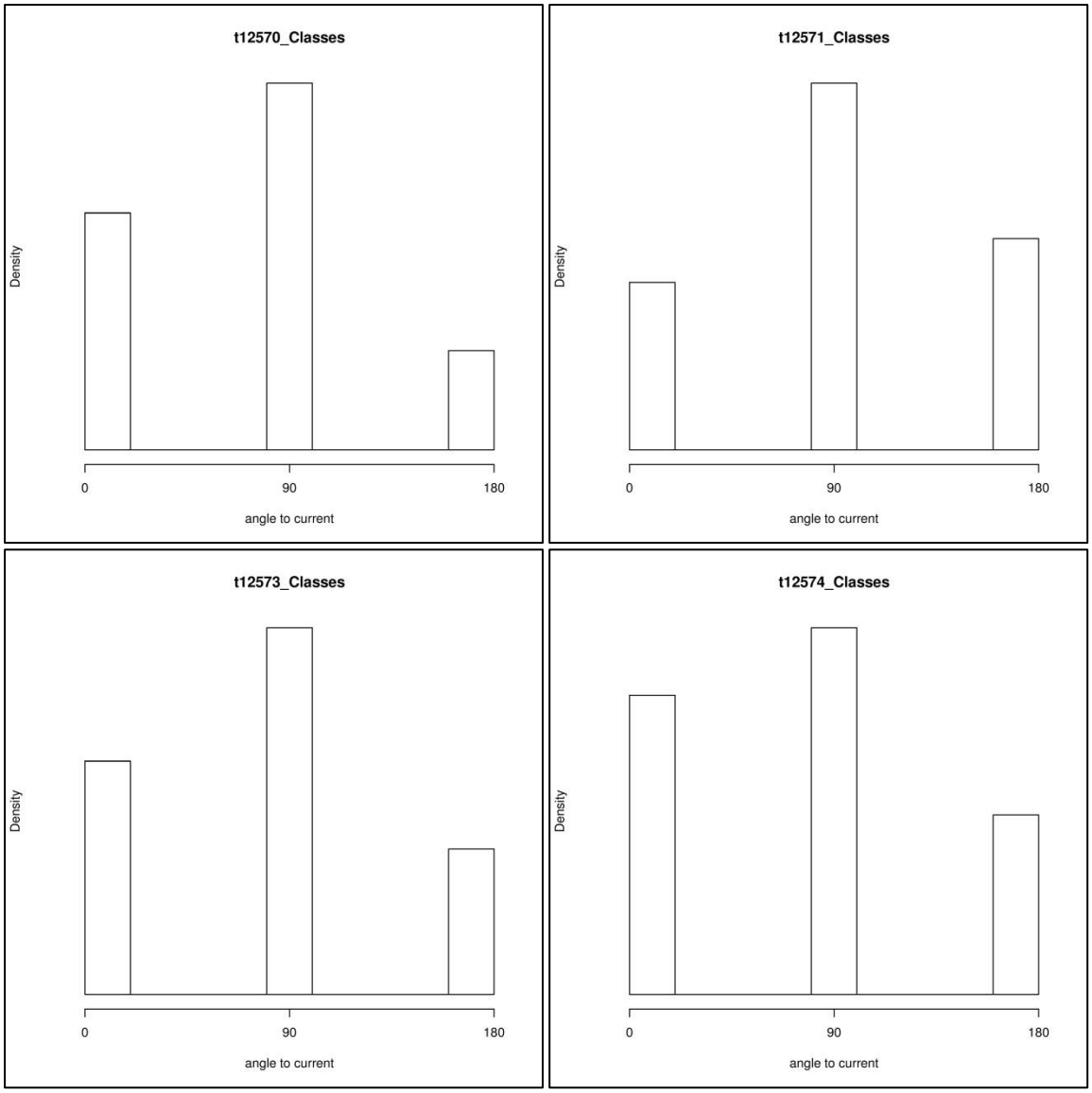


FIGURE 31 – Turtles' angles in relation to ocean currents.

APPENDIX III – General results for the environmental variables

TABLE 1 – Mean values and ranges of the environmental variables for the 10 turtles for all locations, ARS=0 locations and ARS=1 locations

	Bathymetry (m)	SST (^{0}C)	SSH (cm)	SSHA (cm)	|SSHA| (cm)	[Chl*a*] (mg/m^3)	log Chl*a*
ALL LOCATIONS (n= 3202)							
Min	-5620	11.92	-32.61	-43.92	0.001	0.027	-3.62
Max	-2	24.92	72.96	42.11	43.92	15.61	2.74
Mean	-3238	20.36	20.00	2.09	5.40	0.27	-1.87
ARS=0 LOCATIONS (n= 2549)							
Min	-5620	11.92	-30.29	-43.92	0.001	0.027	-3.62
Max	-2	24.92	72.96	42.11	43.92	15.61	2.74
Mean	-3305	20.52	20.48	2.40	5.32	0.27	-1.92
ARS=1 LOCATIONS (n= 653)							
Min	-5332	11.92	-32.61	-43.91	0.01	0.039	-3.24
Max	-45	24.39	55.92	23.22	43.91	8.918	2.19
Mean	2980	19.73	18.10	0.90	5.72	0.325	-1.65

APPENDIX IV – Density histograms for the environmental variables

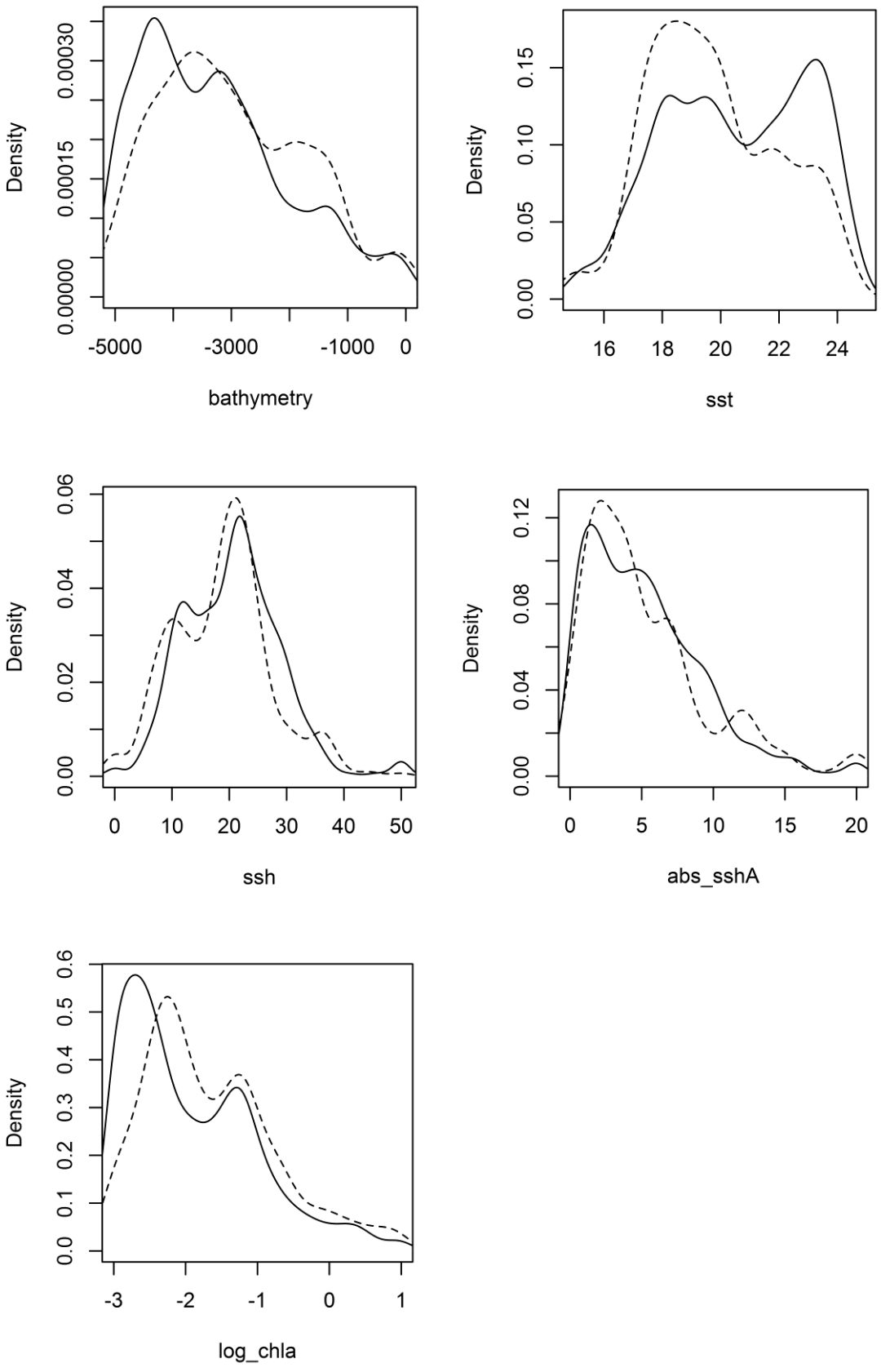


FIGURE 32 – Density histograms for predictor variables in relation to ARS (solid line: ARS=0; dashed line: ARS=1)

APPENDIX V – Pearson's correlation between variables for GAM

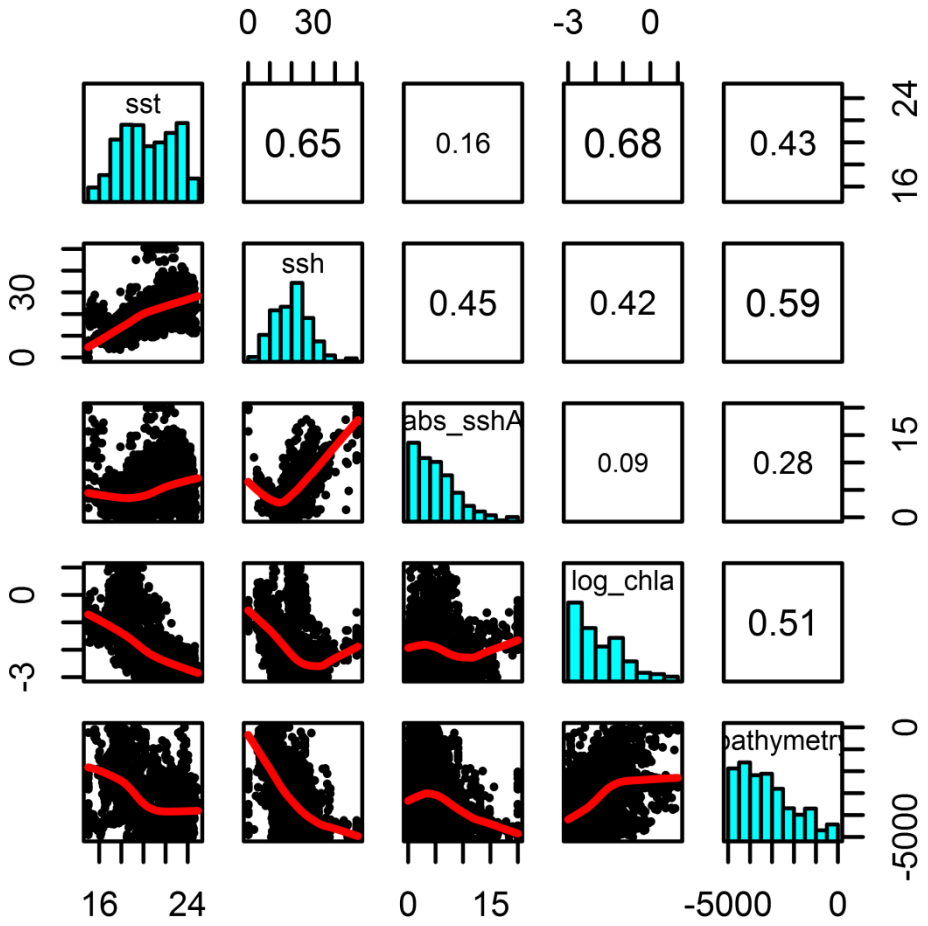


FIGURE 33 – Pearson's correlation between potential variables to fit the GAM; diagonal panels – histograms of the variables' values; lower panels - scatterplot of the two variables and line fitted using the LOWESS smoother; upper panels - Pearson's correlation coefficient for the two variables.

APPENDIX VI – GAM results for training data

TABLE 2 – GAM results on training data:

Approximate significance of smooth terms:

	edf	Ref.df	Chi.sq	p-value
s(ssh)	7.173	7.801	37.89	6.62e-06 ***
s(abs_sshA)	7.743	7.976	50.52	3.17e-08 ***
s(log_chl*a*)	6.93	7.681	47.28	9.90e-08 ***
s(bathymetry)	6.18	7.323	20.05	0.00674 **

Signif. codes: 0 '*' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1**

FORMULA: ars ~ s(ssh) + s(abs_sshA) + s(log_chl*a*) + s(bathymetry)

- R-sq.(adj) = 0.0956
- Deviance explained = 9.55%
- UBRE score = -0.033418
- Scale est. = 1
- n = 2135

GAM results on test data:

MODEL PERFORMANCE SUMMARY:

- Area under the ROC curve (auc) = 0.712
- Mean cross-entropy (mxe) = 0.445
- Precision-recall break-even point (prbe) = 0.388
- Root-mean square error (rmse) = 0.372
- Cutoff selected by maximizing the Youden index = 0.241
- Confusion matrix for that cutoff:

	Actual 1	Actual 0	Total
Predicted 1	133	249	382
Predicted 0	63	620	683
Total	196	869	1065

- Model performance statistics for that cutoff:
- Accuracy (acc) = 0.707
- Error rate (err) = 0.293
- Rate of positive predictions (rpp) = 0.359

- Rate of negative predictions (rnp) = 0.641
- True positive rate (tpr, or sensitivity) = 0.679
- False positive rate (fpr, or fallout) = 0.287
- True negative rate (tnr, or specificity) = 0.713
- False negative rate (fnr, or miss) = 0.321
- Positive prediction value (ppv, or precision) = 0.348
- Negative prediction value (npv) = 0.908
- Prediction-conditioned fallout (pcfall) = 0.652
- Prediction-conditioned miss (pcmiss) = 0.092
- Matthews correlation coefficient (mcc) = 0.317
- Odds ratio (odds) = 5.257
- SAR = 0.597
- Cohen's kappa (K) = 0.287

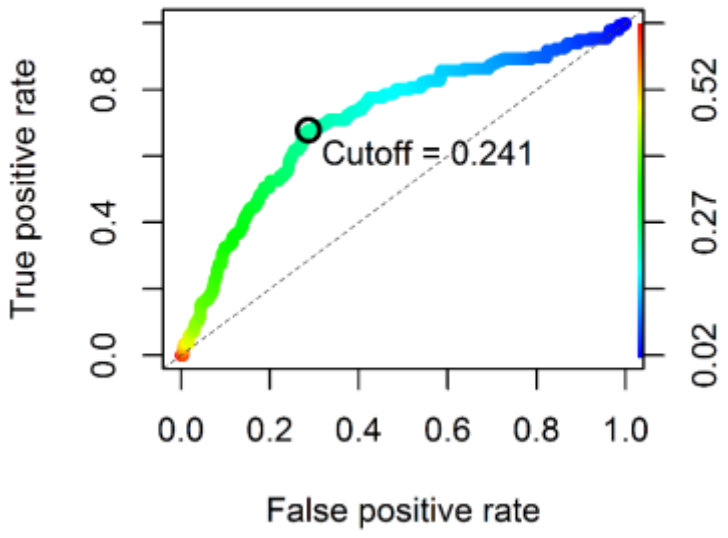


FIGURE 34 – Area under the ROC curve (AUC) and selected cutoff by maximizing the Youden index.